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CONTENTS

Number 1, April 1959

PAGE

Morphology and Physiology of Germination of *Chara gymnopitys* A. Braun. I. Development and Morphology of the Sporeling. By Mary M. Ross .. 1

The Ecology of the Bogong High Plains. I. The Environmental Factors and the Grassland Communities. By Stella G. M. Carr and J. S. Turner .. 12

The Ecology of the Bogong High Plains. II. Fencing Experiments in Grassland C. By Stella G. M. Carr and J. S. Turner 34

Opal Phytoliths in Some Victorian Soils and "Red Rain" Residues. By G. Baker 64

A Contrast in the Opal Phytolith Assemblages of Two Victorian Soils. By G. Baker 88

Number 2, August 1959

PAGE

Control of Water Movement by Stem Chilling. By R. D. Johnston .. 97

Developmental Morphology of the Floral Organs of *Eucalyptus*. I. The Inflorescence. By D. J. Carr and Stella G. M. Carr 109

The Stratigraphy and History of Groenvlei, a South African Coastal Fen. By A. R. H. Martin 142

Studies on the *Sarcomenia* Group of the Rhodophyta. By H. B. S. Womersley and E. Ann Shepley 168

Number 3, December 1959

PAGE

Gastrodia sesamoides R.Br. and its Endophyte. By Ethel I. McLennan .. 225

Chromosome Numbers in the Casuarinaceae. By B. A. Barlow 230

Polyploidy and Apomixis in the *Casuarina distyla* Species Group. By B. A. Barlow 238

Factors Affecting Growth and Distribution of Kauri (*Agathis australis* Salisb.). I. Effect of Light on the Establishment of Kauri and of *Phyllocladus trichomanoides* D. Don. By R. L. Bieleski 252

Factors Affecting Growth and Distribution of Kauri (*Agathis australis* Salisb.). II. Effect of Light Intensity on Seedling Growth. By R. L. Bieleski .. 268

Factors Affecting Growth and Distribution of Kauri (*Agathis australis* Salisb.). III. Effect of Temperature and Soil Conditions. By R. L. Bieleski .. 279

Callitriche in New Zealand and Australia. By R. Mason 295

The Australian Species Referred to *Ichnanthus* Beauv. (Gramineae). By M. Lazarides 328

Index to Volume 7 347

MORPHOLOGY AND PHYSIOLOGY OF GERMINATION OF *CHARA GYMNOPITYS* A. BRAUN

I. DEVELOPMENT AND MORPHOLOGY OF THE SPORELING

By Mary M. Ross*

[*Manuscript received October* 27, 1958]

Summary

A study has been made of the germination stages and development of the protonema of *Chara gymnopitys* A. Braun. The development of this Australian species is compared with that previously described for European and Indian species of the Charales. A detailed account of the sequence of cell divisions prior to the first division of the apical cell of the adult plant is given. The dorsiventral development of the protonemal filament and of the "shoot" is noted. The resulting dorsiventrality of the mature plant is discussed.

The development and structure of the rhizoids is compared with that of the "stem" portion of the plant.

A technique for collecting and germinating *Chara* spores under sterile conditions is fully described.

I. Introduction

Few studies have been made of the stages in germination of the oospore of members of the Characeae and no investigations of this kind have been made on Australian species. Stages in germination of European species were described by several authors in the last century, and very recently details of the development of an Indian species, *Chara zeylanica* Wills., have been published.

Pringsheim (1863), who studied *Chara fragilis* Desv., was the first to elucidate the structure of the proembryo, which had not been clearly understood until then. In 1875 de Bary published an account of oospore development and germination in several European species of *Chara*, *Tolypella*, and *Nitella* in which he reviewed the previous work of Pringsheim, Nordstedt, and Kamicuskis, and presented his own observations. He stated that the course of development is essentially the same in all species of these genera except for the production of minor differences in form. However, some differences from de Bary's schema have been observed in the sequence of development of the protonemal filament of *Chara gymnopitys* A. Braun, which is similar to that described by Sundaralingham (1954) for the Indian species *Chara zeylanica* Wills.

All previous authors (Pringsheim 1863; de Bary 1875; Sundaralingham 1954) have had to rely on the collection of sporelings occurring sporadically in the mud of aquaria or ponds because they were unable to control the germination of clean spores. Following the development of a method of germinating the spores of *Chara gymnopitys* (Carr, unpublished data) large numbers of sporelings of all stages have been available for study, and the results are presented in this paper.

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II. MATERIALS AND METHODS

Mature oospores were collected in mud which was dredged from the bottom of an artificial pond in which *Chara gymnopitys*, originally collected from a pool at Frankston, Vic., had been growing for several years. The mud was washed through a series of sieves to remove particles of soil and debris larger than the oospores, and finer particles were removed by flotation. The remaining mixture of sand grains and empty and viable oospores was then dried and, with the aid of a binocular dissector, the viable oospores were separated from it with a fine brush.

These clean spores were then germinated by a method which will be described in greater detail in another communication. Briefly, the method involves a preliminary sterilization with sodium hypochlorite (5 per cent., 30 min), followed by suspension in water in an evacuated Thunberg tube. After 8–10 days in continuous light at 21°C spores begin to germinate, and after 40 days 50–80 per cent. have germinated.

III. STAGES IN GERMINATION; DEVELOPMENT OF THE RHIZOIDS AND PROTONEMAL FILAMENT

The structure of the mature *Chara* oospore is well known (Fritsch 1948). It consists of a simple cell densely packed with large starch grains and fat globules. It has a pale brown, cellulose wall inside the colourless oogonial wall. This in turn is enclosed in an outer coat formed from the thickened inner walls, and part of the lateral walls, of the five rows of cells which enclose the developing ovum. These cell rows become spiral during the maturation of the zygote. The outer walls, the outer part of the lateral walls, and the contents of these cells disintegrate. The remains of the lateral walls form spiral ridges which meet at the apex of the oospore (Fig. 1). During germination, the tips of these spiral ridges split apart, forming an aperture surrounded by five valve-like projections (Fig. 2). This is the first externally visible sign that germination has begun, but prior to this, changes have already taken place in the internal organization of the oospore. According to Oelkers (1916), whose work has not yet been confirmed, meiosis takes place in the oospore before it opens at the apex so that just before germination the oospore has four nuclei. He states that three of these nuclei eventually disintegrate and the fourth is to be found in the densely granular mass of protoplasm which accumulates at the apex of the oospore as germination commences. This mass of protoplasm is cut off from the base of the oospore by a wall formed at right angles to the longitudinal axis of the oospore and then forms a lens-shaped cell (first node cell of de Bary, Fig. 3). The supposedly enucleate base of the oospore undergoes no further divisions and functions only as a food store for the young sporeling.

The slight upward extension of the first node cell is responsible for the splitting open of the valves of the outer spore coat. The first node cell at first appears through the aperture as a single dome-shaped cell (Fig. 3) which soon becomes divided by a wall either parallel with or inclined at an angle to the longitudinal axis of the oospore (Fig. 4). The two cells thus formed are the primary rhizoid cell and the primary protonemal cell, but they are indistinguishable until further development occurs (Figs. 5, 6). The protonemal cell extends by apical growth into a blunt colourless cylindrical filament before undergoing further divisions (Fig. 9). The rhizoid cell on the other hand undergoes almost immediately a series of irregular divisions to form a mass of wedge-shaped cells (Fig. 7). These wedge-shaped cells usually extend to form subsidiary rhizoids but occasionally one or two form subsidiary protonemata which develop in the manner described below for the main protonema. The primary rhizoid cell and the subsidiary rhizoid cells extend to form colourless cylindrical filaments.

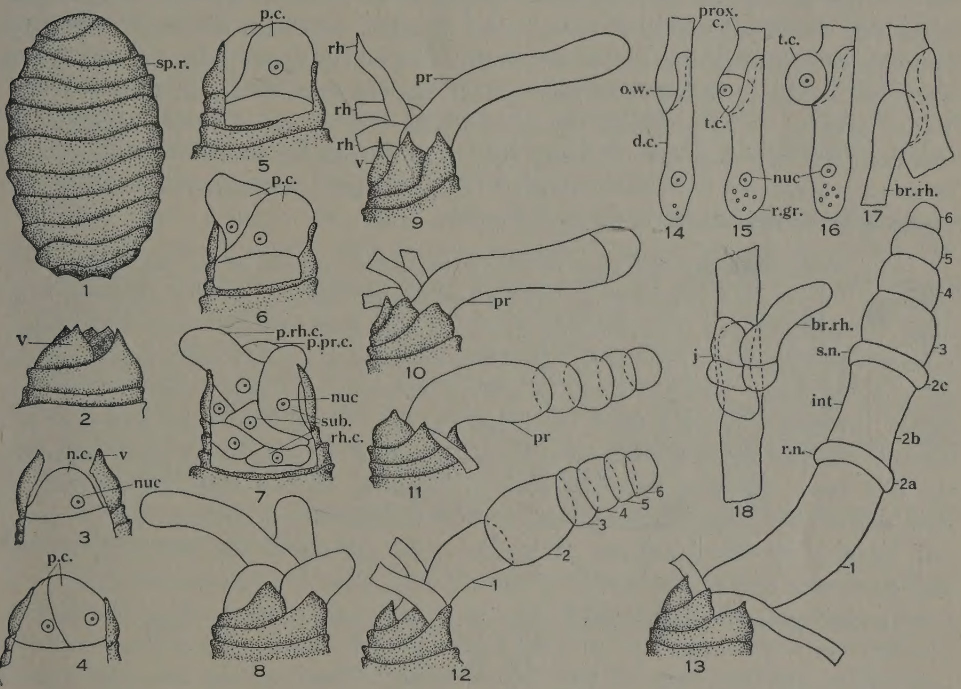


Fig. 1.—The mature oospore, showing the external view. × *c.* 20. *sp.r.*, Spiral ridge. Fig. 2.—The apex of an oospore with open valves. × *c.* 25. *v.*, valve. Fig. 3.—The apex of an oospore with part of the outside wall removed, showing the first nodal cell. × *c.* 25. *n.c.*, First nodal cell; *nuc*, nucleus. Figs. 4–6.—The apex of an oospore with part of the outside wall removed, showing the development of the primary rhizoid and primary protonemal cells. × *c.* 25. *p.c.*, Primary cell. Fig. 7.—The apex of oospore with part of the outside wall removed, showing the developing subsidiary rhizoid cells. × *c.* 25. *p.pr.c.*, Primary protonemal cell; *p.rh.c.*, primary rhizoid cell; *sub.rh.c.*, subsidiary rhizoid cell. Figs. 8–13.—The development of rhizoids and protonema. × *c.* 20. *int*, internodal cell; *pr*, protonema; *rh*, rhizoid; *r.n.*, "root node"; *s.n.*, "shoot node". Numerals in Figs. 12 and 13 refer to the cells of the protonemal filament, which have been numbered acropetally. Figs. 14–18.—The development of "joint" in rhizoid. × *c.* 40. *br.rh.*, Branch rhizoid; *d.c.*, distal cell; *j*, joint; *o.w.*, oblique wall; *prox. c.*, proximal cell; *r.gr.*, refractive granules; *t.c.*, third cell.

It is not always possible to distinguish at this stage between the filaments formed by the primary rhizoid cell and those formed by subsidiary rhizoid cells, without removing the spore coat (Fig. 8). Very often, however, the filaments formed by the primary cells extend sooner than those formed by the subsidiary cells and then may be distinguished by their greater length.

The rhizoids extend very rapidly and become long, narrow filaments, vacuolate except at the tips, where there is a concentration of densely granular cytoplasm. The nucleus is quite conspicuous and is usually to be found lying within the granular cytoplasm directly behind the apex, which is often somewhat swollen. Refractive granules can also be observed in the protoplasm at the apex (Figs. 14–16). These were also noted by Sundaralingham (1954), and he presumed that they were the bodies referred to as statoliths by Giesenhagen (1901) and Schröder (1904). In the vacuolate region of the rhizoids very rapid streaming of the protoplasm was frequently observed, but there appeared to be little movement in the denser protoplasm surrounding the nucleus at the apex.

As the rhizoids develop they branch in a manner typical of the members of the Charales. A swelling is formed in the wall of the rhizoid just behind the apex. An oblique, S-shaped wall then develops in such a way that two cells with overlapping, tapered end walls are formed (Fig. 14). The swollen region forms part of the proximal cell thus delimited from the apex. A second, curved wall forms around the swollen region, dividing it off as a third cell (Figs. 15, 16). Often the second wall does not intersect the first wall and even when it does the third cell never completely separates the first two. The first two cells always remain in contact with one another, at least where the upward-tapering end wall of the distal cell overlaps the proximal cell. Part of the third cell lies within the lower portion of the proximal cell and part protrudes beyond the profile of the rhizoid. This cell may extend directly to form a single branch rhizoid (Fig. 17) but usually undergoes a series of divisions. The first two walls formed are at right angles to each other, one transverse and one longitudinal, dividing the cell into four sections. These sections may also extend directly to form branch rhizoids (Fig. 18) but quite frequently undergo a series of irregular divisions to form a cluster of cells which is often referred to as a "joint". Branch rhizoids usually develop from these cells but they are also capable of producing protonemata. The branch rhizoids themselves branch as they extend, thus forming a series of "joints" situated at intervals along the rhizoids (Plate 2, Fig. 4). This formation has been likened by some authors to the node and internode structure of the "stem".

Normally the rhizoids remain colourless but if they are exposed to light they are capable of developing chloroplasts, though not in such large numbers as are found in the upper regions of the plant. These chloroplasts lie in widely spaced rows which form long spirals along the length of the rhizoid cell. They are often somewhat larger than those found in the "leaves" or "stem" but like these tend to remain stationary close to the wall, and are only occasionally transported along the cell even when the protoplasm is streaming rapidly around the vacuole.

The development of the protonema takes place at the same time as that of the rhizoids. It increases in length, although not as rapidly as the rhizoids, and also increases slightly in thickness (Fig. 9). The cytoplasmic contents become aggregated in the distal part of the filament and the proximal part becomes vacuolate. According to de Bary the distal, densely cytoplasmic portion is then separated off by a transverse wall as a cell which is later divided into two or three cells by transverse wall formations. Sundaralingham (1954), however, states that in *Chara zeylanica*, the first wall is formed directly behind the tip and later walls appear in succession behind the first wall. Close study of *Chara gymnopitys* has shown that in this species the sequence of divisions agrees with that described by Sundaralingham for *Chara zeylanica* and not with that described by de Bary for the European species. In *Chara gymnopitys* the cells are cut off basipetally by transverse walls dividing the protonemal filament into several, usually six units (Figs. 10–12). This filament is of limited apical growth and future divisions occur only in the proximal region. The future "shoot" apex will be developed laterally on it.

The side on which the apical cell will appear is referred to by Pringsheim (1863) as the "front side". This term is retained in the following description. Its meaning may better be apprehended by using an analogy. Imagine the protonemal filament to be represented by a finger of a hand placed palm downwards. The joints of the finger represent the cells of the filament and a ring on the finger may then be taken to represent the ring of peripheral cells in the complex "shoot node", the thicker "front edge" being the shoulders of the ring. The diamond in the bezel will be the apical cell of the shoot. The terms left and right are used in the sense that they would be used by the owner of the hand.

For convenience in description the cells of the protonemal filament have been numbered acropetally (Fig. 12).

IV. FURTHER DEVELOPMENT OF THE CELLS OF THE PROTONEMAL FILAMENT

(*a*) *Cell No.* 1

The last wall in the series delimits the basal cell. The basal wall of this cell is, of course, the one which was formed first in the developing embryo, separating it from the store of food in the remains of the oospore. The basal cell extends slightly in length and considerably in width but does not divide. In a normal plant it remains colourless and does not usually grow above the substratum, but it is capable of becoming green. During the development of the first whorl of "leaves" the basal cell contains many large starch grains similar to those in the ungerminated oospore.

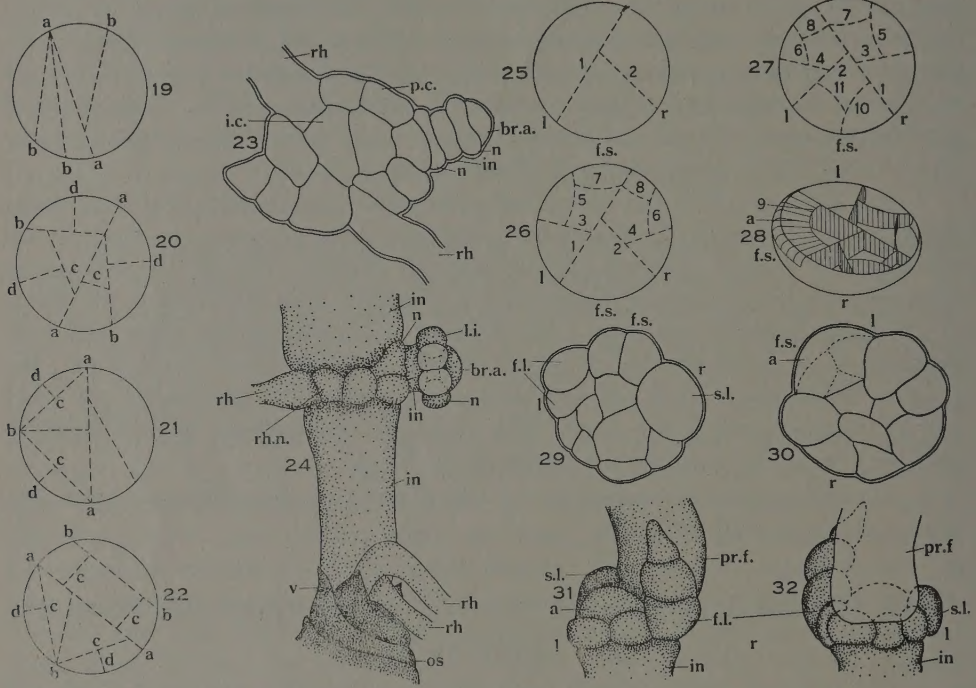
(*b*) *Cell No.* 2

This cell divides twice by transverse walls into three cells (Fig. 13): cell 2*a* (a narrow nodal cell next to cell 1), cell 2*b* (a larger internodal cell), and cell 2*c* (a narrow cell next to cell 3).

(i) *Cell* 2a.—This cell may give rise to accessory branches but generally forms a collection of subsidiary rhizoids and hence is referred to as the "rhizoid node cell".

Initially it is a single discoid cell with a slightly convex outside wall which protrudes beyond the profile of the filament (Plate 1, Fig. 3). It develops into a single layer of cells forming a disc consisting of several central cells surrounded by a single ring of peripheral cells. The arrangement of the walls which subdivide the discoid cell varies greatly in different individuals and, unlike the segmentation of the upper nodes, follows no rigid pattern.

The first wall (*aa*, Figs. 19–22) divides the cell into two often unequal segments. These two cells may then be subdivided simultaneously, although quite frequently one remains undivided for some time while the other undergoes several divisions. These divisions are very irregular and the sequence and patterns of segmentations of the two semi-cells appear to bear no relation to one another, so that only very general statements can be made about them.



Figs. 19–22.—Diagrams showing the sequence of divisions in the rhizoid node cell. × *c.* 35. *aa*, First dividing wall; *b*, first-order wall; *c*, second-order wall; *d*, third-order wall. Fig. 23.—Drawing of a transverse section of a mature rhizoid node, showing an accessory branch "bud". × *c.* 40. *br.a.*, Accessory branch apical cell; *i.c.*, internodal cell; *in*, internode; *n*, node; *p.c.*, peripheral cell; *rh*, rhizoid. Fig. 24.—Lower region of the sporeling, showing the position of the rhizoid node and the accessory branch "bud" with "leaf" initials. × *c.* 30. *l.i.*, "Leaf" initial; *n*, node; *os*, oospore; *rh*, rhizoid; *v*, valve; *rh.n.*, rhizoid node. Figs. 25–27.—Diagrams showing the sequence of division in the "shoot" node. × *c.* 35. Walls numbered in order of formation: *f.s.*, "front" side; *l*, "left" side; *r*, "right" side. Fig. 28.—Diagram of the "shoot" node, showing the swollen "front" side and the apical cell. × *c.* 40. *a*, Apical cell. Fig. 29.—Drawing of the "shoot" node: basal view showing the complete ring of peripheral cells and the first division of the first "leaf" initial and the enlarging second "leaf" initial. × *c.* 40. *f.l.*, First "leaf" initial; *s.l.*, second "leaf" initial. Fig. 30.—Drawing of the "shoot node" viewed from above, showing the dome-shaped apical cell. × *c.* 40. Fig. 31.—"Shoot node" "front" view. × *c.* 25. *pr.f.*, Protonemal filament. Fig. 32.—"Shoot node" "back" view. × *c.* 25.

The first-order walls (*b*, Figs. 19–22) may be parallel with the original dividing wall but more frequently they are inclined towards it or intersect it, forming one or two wedge-shaped cells, and one or two more or less lens-shaped cells on the outside of the disc. Usually the wedge-shaped cells are each divided by roughly tangential second-order walls (*c*, Figs. 19–22) into one or two peripheral cells and one internal cell. If the peripheral cells are sufficiently large they are subdivided by radial or third-order walls (*d*, Figs. 19–22). The lens-shaped cells are also subdivided by third-order radial walls completing the ring of peripheral cells. The central cells remain undivided. The peripheral cells generally extend directly and become rhizoids (*rh*, Figs. 23, 24).

Unlike the plant illustrated in de Bary's (1875) text, *Chara gymnopitys* does not usually produce accessory protonemata from the peripheral cells. However, these cells may be further subdivided by means of transverse walls and then become the initial cells of accessory branches (Figs. 23, 24). These accessory branches are similar to those described by Drew (1926) for *Nitella opaca.* Their development differs from that of accessory protonemata. The initial cell divides by transverse walls to form a tier of four cells. The first cell in the tier is a nodal cell which forms a single-layered, multicellular disc similar to that of the rhizoid node on which it is borne; the peripheral cells, however, do not immediately extend to form rhizoids or further branches. The second cell of the tier is an internodal cell similar to cell 2*b* described below. The third cell is a nodal cell which forms the first whorl of "leaves" of the branch. The fourth cell is the apical cell by which the branch is potentially capable of further growth. In a normal plant, after the formation of the "leaves" the branch usually ceases to grow and the apex remains dormant for some time. It is capable of further development should the main axis be damaged, and its behaviour is therefore similar to that of a dormant bud.

(ii) *Cell* 2b.—This cell extends considerably to form a long internodal cell but, unlike the upper internodal cells of the mature plant, becomes corticated. If it is not buried below the surface of the mud it may become green.

(iii) *Cell* 2c.—This cell, known as the "shoot node cell", is first formed as a discoid cell with a convex outer wall and initially resembles the rhizoid node cell. Before dividing, it becomes swollen on the "front side" (the shoulders of the ring, using the analogy given on page 5) and protrudes beyond the profile of the adjacent cells (Plate 1, Fig. 3). This causes the upper part of the filament, composed of cells 3, 4, 5, and 6 (Fig. 13), to bend at an angle to the main axis of the protonema.

De Bary (1875) states that he was unable to decide whether the shoot node cell was initially formed as a wedge-shaped disc, or as a flat one. However, in sporelings of *Chara gymnopitys* observed directly after the initiation of cell 2*c*, no lateral swelling of this cell is apparent. It divides more rapidly than the rhizoid node cell and frequently has formed a multicellular plate before the latter has undergone more than one or two divisions.

The divisions observed in this cell are generally similar to those described by de Bary and support his contention that Pringsheim's early observations were inaccurate.

The first division, according to de Bary, is by a longitudinal wall which passes centrally through the swollen "front side", dividing the cell into more or less equal halves. In *Chara gymnopitys,* however, wall No. 1 (Fig. 25) does not pass centrally through the "front side" but begins some distance to the left of the thickest region and passes diagonally across the cell, dividing it into two unequal sections. Wall No. 2 (Fig. 25) is formed to the right hand of the "front side" and intersects the first, somewhat behind the central axis of the disc, cutting off the thickest region of the disc in the form of a wedge. The succeeding walls are formed on alternate sides, cutting off cells which become progressively smaller as the rear portion of the disc is approached. Wall No. 3 is formed on the left side and intersects wall No. 1 (Fig. 26); No. 4 on the right intersects No. 2; No. 5 on the left intersects No. 3; No. 6 on the right intersects No. 4. The next two walls (Nos. 7 and 8) are internal, periclinal divisions delimiting internal from external cells in the disc (Figs. 27, 29).

Occasionally slight variations have been noticed but generally the pattern of cell formation in the disc is very regular. The first wedge-shaped cell, which is much larger than the others, becomes the apical cell of the mature plant. It enlarges rapidly, bulging upwards and outwards, and at an early stage forms a conspicuous dome surrounded by the ring of smaller peripheral cells of the disc (Figs. 30–32). These peripheral cells develop into the rudimentary "leaves" of the "shoot node". The relative size of the peripheral cells is reflected in the ultimate size of the members of the whorl. Those formed from the first-formed, larger cells develop first and always become larger than those formed from the smaller cells (Plate 2, Figs. 1–4).

(*c*) *Cells Nos.* 3, 4, 5, *and* 6

The remaining three or four cells of the filament undergo no further divisions. The ultimate cell, No. 6 (Fig. 13), becomes conical in shape and extends only slightly in length and breadth while the other two or three cells extend considerably in length and breadth. Together these cells form a filament which, by reasons of development consequent on the activity of the apical cell, is constrained to an apparently lateral position. This filament then takes its place as a member of the "shoot node" whorl. It develops chloroplasts, but even in the mature plant is usually distinguishable from the other members of the whorl by its greater length and lack of stipules (Plate 2, Figs. 2, 4).

(*d*) *The Apical Cell*

The first division of the apical cell is transverse to the axis of the plant but oblique to the "front side" No. 9 (Fig. 28). This wall cuts off the bulging "front" surface from a cell which remains within the disc and is referred to by de Bary as the "first node cell" of the mature plant. This node cell is later subdivided into three—an inner cell and two peripheral cells. The two peripheral cells complete the peripheral ring of the shoot node and are cut off by walls convex towards the centre of the disc (Figs. 27, 29, 30). The first wall intersects wall No. 1 and the outside wall, the second intersects the first and wall No. 2. These two cells eventually form rudimentary "leaves" as part of the "shoot node" whorl. The inner cell remains undivided in the centre of the "shoot node".

The now dome-shaped apical cell (Figs. 29, 31, 32) continues the growth of the mature plant.

V. DISCUSSION

(1) Except for relatively minor differences the morphology of germination and the development of the protonema of *Chara gymnopitys* A. Braun is similar to that of the European species *C. foetida* A. Br., *C. fragilis* Desv., *C. contraria* A. Br., *C. crinita* Wallr., and *C. scoparis* Baur., described by de Bary (1875), and of the Indian species *C. zeylanica* Wills., described by Sundaralingham (1954).

During the development of the protonemal filament the sequence of wall formations differs from that described by de Bary but is in accord with that described by Sundaralingham. In *C. gymnopitys* and *C. zeylanica* the first wall is formed directly behind the tip of the protonemal filament and successive walls are formed basipetally. These walls form in very rapid succession and it was only after observing many specimens that the sequence of wall formations could be determined with certainty. It is therefore not inconceivable that de Bary was in error in stating that the first-formed wall is the most proximal one and separates off the distal, densely cytoplasmic portion of the filament, which is later divided into several cells. The only other difference from de Bary's schema is that in the formation of the "shoot" node the first dividing wall does not form centrally (as he states) but to the "left" of the bulging "front side".

(2) As yet Oelkers's (1916) work on the meiotic divisions of the nucleus, which he states to occur prior to germination, has not been confirmed. Attempts have been made to observe the nuclear condition of the germinating oospore, but owing to the very small size of the nuclei and the presence in the spore of very numerous and large starch grains, and the tough impregnable nature of the spore coat, a satisfactory technique for studying the nuclei has not yet been devised. Further attempts to confirm that the meiosis takes place immediately prior to germination are in progress.

(3) It is not known yet what factors determine which of the original two cells formed by the first longitudinal wall in the first node cell will develop to form the rhizoid portion, and which the "stem" portion of the plant. In the early stages of development these two cells are identical in outward appearance, and it is not possible to distinguish which is the primary rhizoid and which the primary protonemal cell until they undergo further divisions. This matter also requires further investigation.

(4) Although some authors have likened the structure of the rhizoids, with their series of "joints" situated at intervals, to the node-and-internode structure of the "stem", it is apparent from the study of the development of the "joints" that this similarity is quite superficial. However, the ability of the rhizoids to develop chloroplasts on exposure to light, and also the not infrequent development of subsidiary protonemata from the "joints", indicate that at least in some respects

the rhizoids cannot be considered as being completely dissimilar to the "stem" portion of the plant.

(5) It is clear from the study of the development of the protonema and the first whorl of "leaflets" that the "stem" of this plant is dorsiventral, and not radially symmetrical as would appear at first glance. Dorsiventrality is first indicated by the asymmetrical growth of the "shoot node" cell, which becomes swollen on one side, the "front side", and protrudes beyond the profile of the adjacent cells. Referring again to the analogy of the finger of a hand, dorsiventrality of the protonemal filament is not evident until the unilateral swelling of the "shoot node" cell (at the "knuckle" of the finger) defines the position of the hand as "palm upwards" or "palm downwards".

Later indications of dorsiventrality are to be seen in the difference in age and size of the "leaflets" in each whorl. Those which are formed on the "front side" of the "stem" are formed first and are usually slightly longer than the subsequently formed members of the mature whorl.

Dorsiventrality is further shown during the development of sex organs in the mature plant; the sex organs are formed first on the oldest members of the whorl. It is not yet possible to state when the dorsiventrality of the plant is determined during development, or what factors are involved in its determination. Further work is planned to investigate these problems.

VI. Acknowledgments

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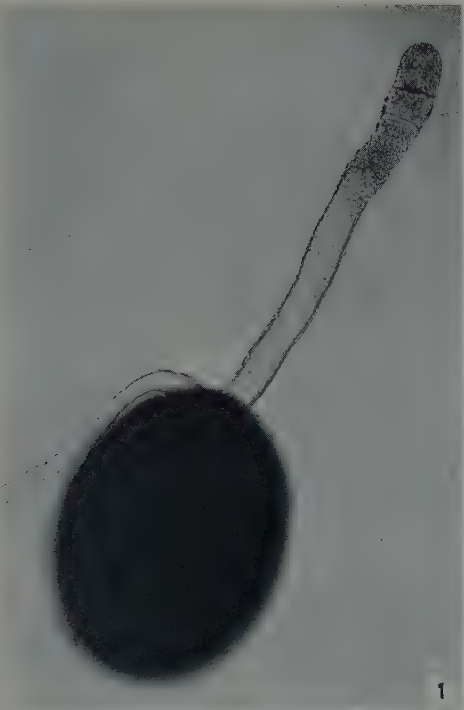
GERMINATION OF C. GYMNOPITYS. I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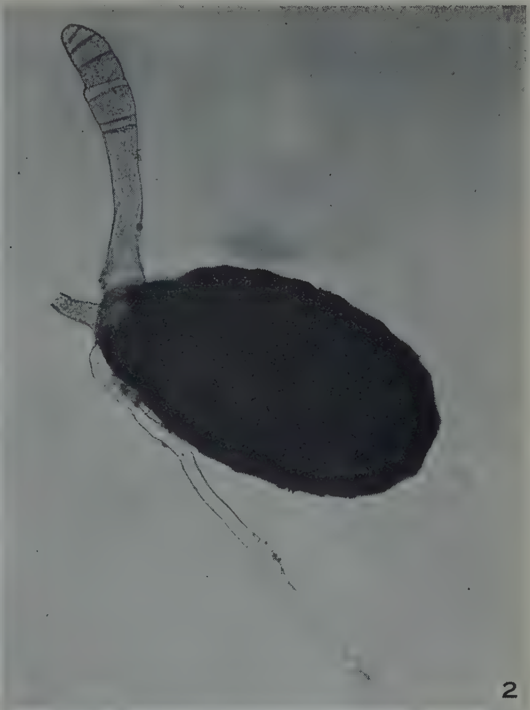
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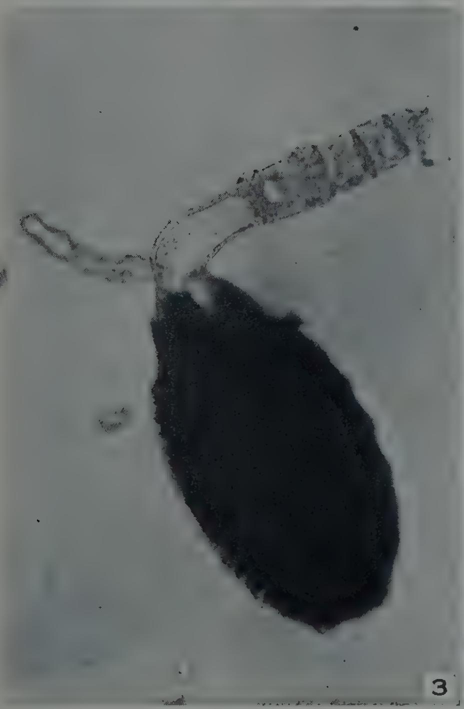
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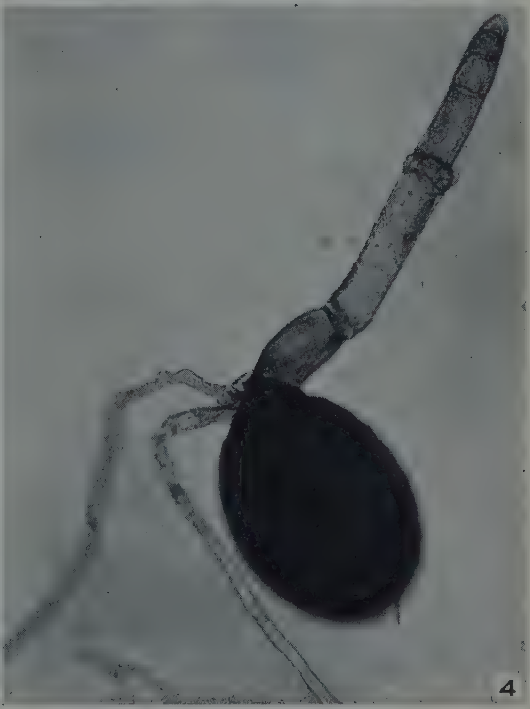
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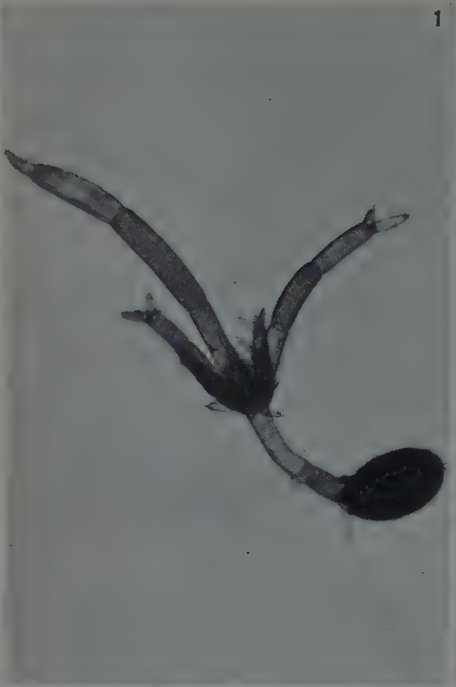
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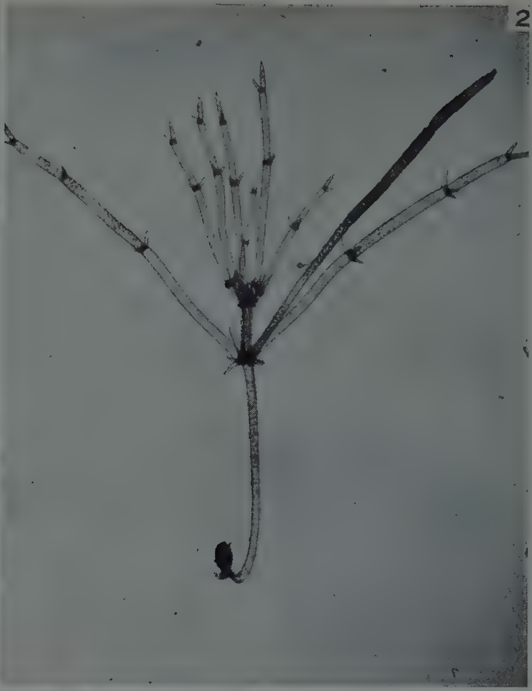
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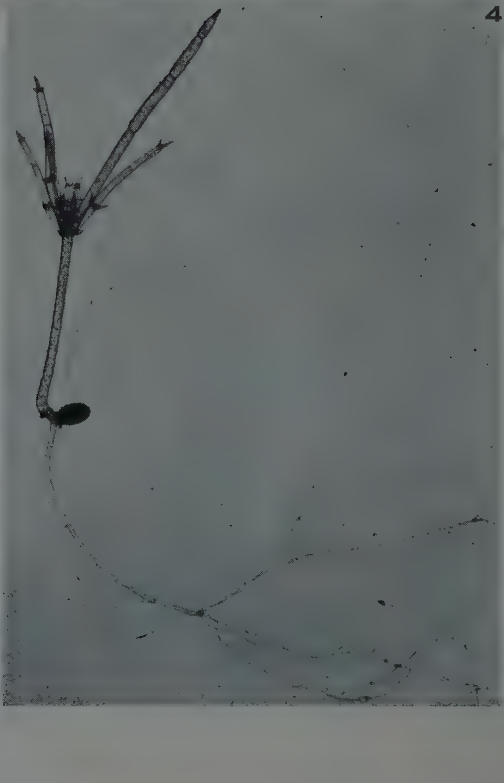
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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—Germinating spore, showing the protonemal filament with the densely cytoplasmic distal portion undergoing a series of basipetal divisions. The fourth transverse wall of the series is just visible. × *c.* 80.

Fig. 2 and Fig. 3.—The protonemal filament at the 8-cell stage, showing the development of the rhizoid node cell and the "shoot node" cell. The "shoot node" cell with its swollen "front side" is shown clearly in Fig. 2. × *c.* 100.

Fig. 4.—The protonemal filament, showing the extension of the internodal cells and the development of "leaf" initials on the "shoot node". × *c.* 70.

Plate 2

Fig. 1.—The dorsiventral "shoot node" whorl. The larger first-formed "leaves" are on the "front side" of the "stem". The protonemal filament is distinguishable by its size and lack of stipules. A "bud" is visible on the rhizoid node. × *c.* 30.

Fig. 2.—An older plant, showing the extension of cell *2b* (ref. Fig. 13). The protonemal filament is distinguishable from the other members of the "shoot node" whorl by its lack of stipules. × *c.* 10.

Fig. 3.—The dorsiventral "shoot node" whorl and a branch "joint" on the greatly extended primary rhizoid. × *c.* 30.

Fig. 4.—The rhizoid system, showing the series of branch "joints" situated at intervals along the rhizoids. × *c.* 10.

THE ECOLOGY OF THE BOGONG HIGH PLAINS

I. THE ENVIRONMENTAL FACTORS AND THE GRASSLAND COMMUNITIES

By Stella G. M. Carr* and J. S. Turner†

[*Manuscript received November 19, 1958*]

Contents

		Page
	Summary	12
I.	Introduction	12
II.	Factors affecting the vegetation	15
	(*a*) Climate	15
	(*b*) Biotic factors	18
	(*c*) Fire	22
III.	The important plants of the grassland, their field behaviour and reactions to grazing	23
	(*a*) *Poa australis*	23
	(*b*) *Carex hebes*	25
	(*c*) Herbs	26
	(*d*) The pattern of grazing	26
IV.	The grassland communities	27
	(*a*) Grassland A	28
	(*b*) Grasslands B and B_1	29
	(*c*) Grassland C	30
	(*d*) Grassland D	32
V.	Acknowledgments	32
VI.	References	32

Summary

The paper is the first of several to present the results of a study, over the last 12 years, of alpine vegetation of the Bogong High Plains (north-eastern Victoria, 5400–6200 ft elevation). Attention is focused on the grassland communities and the response of soils and vegetation to the exclusion of cattle grazing. The first paper outlines the problem, briefly describes the major grasslands, and discusses the climatic and biotic factors concerned.

I. INTRODUCTION

The Bogong High Plains (Fig. 1), the largest of the alpine plateaux of north-eastern Victoria, are set among the highest of the Victorian mountains. From whichever direction they are approached one must climb steep slopes through forests of woollybutt (*Eucalyptus delegatensis*)‡ and diminishing thickets of snow

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† Botany School, University of Melbourne.

‡ The full names and authorities of the plant species mentioned are given in Appendices I and II of paper II in this series.

gum (*E. pauciflora*) before the sweeping expanse of brown grassland is reached at about 5400 ft.

The area of the High Plains embraces about 30 square miles. The impression of greater expanse is due partly to the meandering shape of the area and partly to the difficulties of travel within it. The main plateau is long and narrow, and is extended by the great spurs which arise from it. Some of the spurs are higher than the main top and the others fall away only gradually from it. The hills of metamorphic and plutonic rocks are for the most part rounded and smooth (Mount Nelse, Spion Kopje, Mount Hotham—Plate 1, Fig. 1), but some are rocky and irregular (Mount McKay and Mount Cope—Plate 1, Fig. 2). Those which are capped by the columnar Older Basalt are flat-topped and have steep sides (Mount Jim, Mount Loch, Basalt Hill).

The High Plains are by no means as level as the name suggests, but range in elevation from 5400 ft at Rocky Valley to 6169 ft at Mount Nelse North. All the valleys of the area are wide and shallow and the two largest, Rocky Valley and Pretty Valley, are occupied by streams which are the main tributaries of the East Kiewa River. On the High Plains these streams and the others which drain the area meander on flat grades in shallow, peaty alluvium, but once they leave the High Plains they flow in steep immature valleys.

The hillsides and other well-drained sites mostly carry grassland, dominated by *Poa australis* var. snow grass, but in exposed situations, or where accelerated erosion has taken place, shrubs or perennial herbs are abundant and often dominate communities which form an irregular mosaic with the grassland. The treeless areas are bordered by snow gum woodlands. Snow gum also occurs on the tops and slopes of some of the rocky hills of the main plateau, as, for instance, on Mount Cope and the hills which form the watershed between Rocky and Pretty Valleys. It is absent from the tops and the exposed slopes of the higher smooth mountains and from the flat expanses of Older Basalt. The trees of the woodlands are small and gnarled and usually branched from the base. Where the woodlands are in their natural state they are open and the field layer is dominated by snow grass, which extends right up to the bases of the trees (Plate 2, Fig. 1). Where the woodlands have been burnt the dead trunks and branches of the trees form a tangle among the regrowth from the lignotubers; shrubs occur beneath and among the trees and the trunks are commonly surrounded by bare ground (Plate 3, Fig. 1).

In all the wet places on the High Plains there are peaty areas, known as mossbeds. These carry a particularly rich and varied flora, rooted in an acid peat made up of *Sphagnum leionotum* and the dead remains of higher plants. The most prominent of these belong to the families Restionaceae, Cyperaceae, Liliaceae, Epacridaceae, and Myrtaceae. From a distance the mossbeds take on the brownish colour of the shrub foliage, which obscures the underlying golden *Sphagnum*.

The smaller mossbeds occur below springs and along the courses of smaller streams. More extensive mossbeds occur in the flat bottoms of the large valleys. Here the streams flow on stony or rocky beds between banks of peat or peaty alluvium up to 10 ft in depth. The slow-flowing streams are continually changing

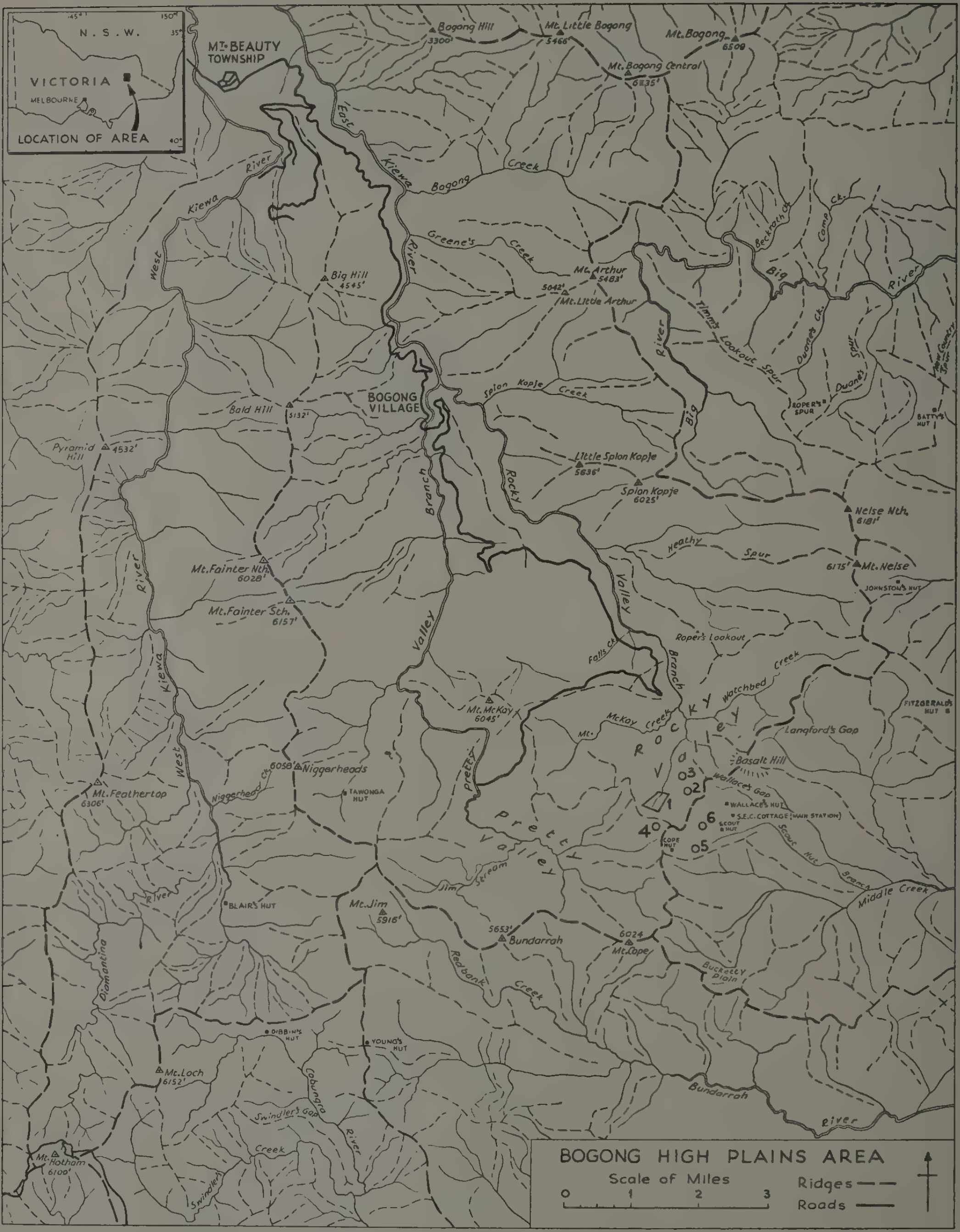
N. S. W.
VICTORIA
MELBOURNE
LOCATION OF AREA
145°
150°
35°
40°
MT. BEAUTY TOWNSHIP
Bogong Hill 3300'
Mt. Little Bogong 5466'
Mt. Bogong 6509
Mt. Bogong Central 6235'
East Kiewa River
Bogong Creek
Kiewa River
West River
Greene's Creek
Big Hill 4545'
Mt. Arthur 5483'
5042'
Mt. Little Arthur
Beckrath Ck.
Camp Ck.
Big River
Timms Lookout Spur
Duane's Ck.
Duane's Spur
ROPER'S SPUR
New Country Spur
BATTY'S HUT
Spion Kopje Creek
BOGONG VILLAGE
Bald Hill 5132'
Pyramid Hill 4532'
Little Spion Kopje 5636'
Spion Kopje 6025'
Rocky Valley Branch
Branch Valley
Nelse Nth. 6181'
Heathy Spur
6175' Mt. Nelse
JOHNSTON'S HUT
Mt. Fainter Nth. 6028'
Mt. Fainter Sth. 6157'
West Kiewa River
Roper's Lookout
Falls Ck.
Watchbed Creek
FITZGERALD'S HUT
Mt. McKay 6045'
Mt. McKay Creek
ROCKY VALLEY
Langford's Gap
Basalt Hill
Wallace's Gap
WALLACE'S HUT
S.E.C. COTTAGE (MAIN STATION)
SCOUT HUT
COPE HUT
Scout Hut Branch
1 2 3 4 5 6
6058' Niggerheads
Niggerhead Ck.
TAWONGA HUT
Mt. Feathertop 6306'
Pretty Valley
Jim Stream
BLAIR'S HUT
Mt. Jim 5916'
5653' Bundarrah
6024 Mt. Cope
Middle Creek
Redbank Creek
Buckety Plain
Diamantina
DIBBIN'S HUT
YOUNG'S HUT
Mt. Loch 6152'
Cobungra River
Swindler's Gap
Swindler's Creek
Bundarrah River
Mt. Hotham 6100'
BOGONG HIGH PLAINS AREA
Scale of Miles
0 1 2 3
Ridges
Roads

Fig. 1.—Map of the Bogong High Plains, Mt. Bogong, and Kiewa Valleys, showing the location of experimental plots (1–5), which lie approximately in the centre of the area under discussion.

course and bends in the streams may be cut off by the growth of banks of *Sphagnum* (Plate 2, Fig. 2).

The peat of the mossbeds retains water, even in the height of summer. Spongy masses of healthy *Sphagnum* retain up to 24 times their own weight of water. Under natural conditions all the water of the streams leaving the High Plains passed over the surface of, or through, mossbeds. Such streams were free of sediment and their flow was effectively regulated.

The High Plains and similar Victorian alpine areas are the parts of the River Murray catchment which receive the greatest annual precipitation. They also form the major part of the catchment of the Kiewa Hydroelectric Scheme of the Victorian State Electricity Commission. The maintenance of the vegetative cover is, therefore, of great economic importance (Aust. Acad. Sci. 1957). In 1944, one of us (S.G.M.C.) reported to the Soil Conservation Authority that soil erosion was occurring on the High Plains. Severe accelerated erosion had taken place and is still occurring in three main types of country. These are: (*a*) steep wooded slopes which were burnt in 1939 and possibly also in earlier fires; (*b*) steep slopes on which snow drifts lie late (snow patches) (Plate 3, Fig. 2); (*c*) the tops of mountains above the tree line (Plate 3, Fig. 3). Sheet erosion, in some cases advanced to the stage of rill formation, is common on these areas. Gullying is associated with badly eroded snow patches and the sites of former mossbeds.

The surviving mossbeds are much drier than they were even as late as 1925, when it is said that it was impossible to ride a horse through them and, at the best, uncomfortable to walk in them. In many places the peat has dried out and is being washed away and blown away. In most mossbeds there is little active growth of *Sphagnum* and in some the deposition of material carried by the streams has caused the death of the mossbed plants (Plate 3, Fig. 4) (see also Costin 1957).

It was pointed out in 1944 that the most serious but least obvious problem existed in the grassland. Its condition suggested that degenerative changes indicative of the early stages of accelerated erosion had occurred. The poor state of the sward was thought to be primarily due to overgrazing in the past, with fire as a contributing factor. Experimental ecological studies were initiated in January 1945 by S. G. M. Carr, and these have been continued each year since then (excepting 1953 and 1955) under the general supervision of both authors. This first paper deals with climatic and biotic factors, and describes the grassland communities.

II. Factors Affecting the Vegetation

(*a*) *Climate*

(i) *Precipitation*.—The mean annual precipitation (1935–1957) is 95·53 in. The minimum recorded during the period was 51·89 in. (1938) and the maximum 169·23 in. (1956). Table 1 shows that the main incidence is in the winter months with a minor peak in October. The variance for each month is considerable and the precipitation is also known to vary considerably over quite short distances within the area. The winter precipitation is in the form of snow and, although the summer precipitation is mainly rain, snow has been recorded for every month of the year. The area is usually under snow for 4 months (June to September), but both the amount of snow received and the duration of snow cover show wide variations. Data selected to illustrate this are set out in Table 2. In years of heavy snow the general thaw may be delayed until late November or December and snow drifts may then persist until autumn.

TABLE 1

PRECIPITATION: BOGONG HIGH PLAINS, 1935–1957

1935–1946, Bogong High Plains Main Station (daily readings)
1947–1951, Roper's No. 1 Station, Fall's Creek (daily readings)
1952–1958, Roper's No. 1 Station, Fall's Creek (readings not daily)

	Precipitation (in.)												
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean	3·92	5·30	5·02	7·97	8·42	10·19	11·52	12·73	8·40	10·07	7·26	5·52	95·53
Variance	2·82	4·11	3·55	7·35	6·10	6·37	6·91	8·00	3·33	4·95	3·55	3·16	27·48

TABLE 2

MEAN SNOW DEPTHS (IN.): BOGONG HIGH PLAINS (ROCKY VALLEY)

Dates	1935	1936	1937	1938	1939	1940	1941	1946*
June 1	0	2	3	7	0	6	0	—
June 10	5	6	5	10	3	5	3	22·8
June 20	8	8	6	8	3	3	10	24.7
June 30	21	22	5	18	24	1	9	27·0
July 10	25	29	8	27	34	0	14	—
July 20	35	33	20	24	32	10	14	—
July 30	39	36	26	24	29	16	20	—
Aug. 9	51	41	26	29	36	19	28	—
Aug. 19	45	47	26	30	48	23	30	—
Aug. 29	33	57	25	24	64	15	23	—
Sept. 7	28	55	24	21	74	7	14	—
Sept. 17	30	52	21	15	69	0	4	73·5
Sept. 27	16	40	10	2	53	—	11	—
Oct. 7	4	18	0	0	41	—	0	65
Oct. 17	0	8	—	—	25	—	—	42
Oct. 27	—	3	—	—	8	—	—	—

* 1946 Record incomplete.

(ii) *Temperature.*—The temperature records are set out in Table 3.

No frost records are available for the Bogong High Plains. The data set out in Table 4 are for Hotham Heights (5900 ft) (Foley 1945).

(iii) *Evaporation.*—During the summer months (December to February) the mean evaporation exceeds the mean precipitation. Evaporation may also exceed precipitation in October and November (Table 5).

Because the Main Station was situated in a rather sheltered position the evaporation recorded is probably less than that which occurs in those parts of the High Plains exposed to the full force of the prevailing wind.

TABLE 3

TEMPERATURES (°F): BOGONG HIGH PLAINS MAIN STATION, 1935–1946

Month	Maximum Temperatures Recorded			Minimum Temperatures Recorded			Mean Monthly Temperatures Recorded		
	Mean	Lowest	Highest	Mean	Lowest	Highest	Mean	Lowest	Highest
Jan.	75·8	65·9	87·4	29·1	24·4	37·0	53·3	51·1	60·2
Feb.	73·5	66·5	80·0	29·0	24·7	33·0	52·4	49·5	59·6
Mar.	69·0	63·8	80·4	27·1	22·9	29·9	49·3	45·6	56·6
Apr.	61·3	57·6	70·5	22·3	17·6	27·0	41·6	38·0	45·5
May	53·2	47·0	61·8	21·4	18·2	23·1	37·3	34·6	41·0
June	45·7	39·2	49·5	19·9	15·4	24·2	32·0	29·0	35·7
July	43·4	39·2	47·5	17·6	13·7	20·5	29·9	27·0	32·1
Aug.	44·6	38·7	51·3	18·7	16·8	21·5	30·9	27·3	34·2
Sept.	50·4	46·1	55·5	18·9	15·0	22·2	34·4	31·7	37·9
Oct.	59·4	52·6	65·0	22·3	18·0	28·2	40·3	36·3	44·0
Nov.	69·1	62·4	73·1	24·3	18·0	28·8	46·2	43·5	49·6
Dec.	73·8	68·6	78·4	26·8	22·3	30·5	50·6	47·8	53·3

TABLE 4

FROST FREQUENCY: HOTHAM HEIGHTS (5900 FT)

Values represent average number of days per month of minimum screen temperatures of 32°F or under. Average frost-free period, 13 days

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
2·7	2·2	3·6	11·6	15·7	26·3	29·3	26·8	22·8	13·9	7·8	5·1	167·8

The mean monthly evaporation has a much lower variance than that shown by the rainfall.

(iv) *Discussion.*—The most striking feature of the climate is the great variability shown by all factors, which makes it difficult to relate the behaviour of the vegetation to the recorded meteorological data. It is impossible, for instance, to predict the course of development the vegetation will follow on the basis of conditions early in the growing season. To date only general conclusions can be drawn, and these are summarized in Table 6. Evaporation exceeds rainfall in the summer months and shows a much lower variance than the rainfall. In consequence the vegetation is greatly affected by the amount and the incidence of summer rain. For sustained growth and maximum flowering, falls of at least an inch of rain spaced at intervals of not more than 10 days are required. If 3 weeks pass without rain the vegetation begins to look dry and many herbaceous species wilt. Sporadic light showers are of little importance, as much of the water is lost by direct evaporation from the foliage.

TABLE 5

EVAPORATION: BOGONG HIGH PLAINS MAIN STATION, 1935–1946

	Evaporation from Pan (in.)					Evaporation from Snow (in.)				Evaporation from Pan (in.)			Total for Year (in.)
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Mean	7·30	5·70	4·54	2·07	0·88	0·43	0·34	0·31	0·59	3·62	5·66	6·79	38·23
Variance	1·04	1·50	1·09	0·53	0·44	0·21	0·50	0·21	0·27	1·78	0·88	1·22	4·50

Plant response in the summer is also conditioned by the winter climate. Light snow cover in a preceding winter is unfavourable for growth. Presumably this is because less water than usual enters the soil, and also because the vegetation is exposed to desiccating winds and low temperatures at times when it would normally be blanketed by snow. A heavy snow cover during the winter is generally a favourable factor for plant growth, unless the thaw is late or is not accompanied by rain. Rain at the time of the thaw or shortly afterwards has the effect of washing away the mucilaginous material known as "the slimes". This is the debris left on the vegetation by the melting snow. If the slimes remain on vegetation which has been flattened by the weight of snow, the whole mass, which consists largely of dead leaves, is cemented together and the growth of new leaves and shoots is hampered.

(*b*) *Biotic Factors*

(i) *Higher Animals* (*feral*).—No species of higher animal is characteristic of, or restricted to, the open grasslands. Although emus and hares are occasionally seen above the tree line, neither species is abundant now, nor is either believed to have been numerous in the past. Wombats and rabbits may be found just below the tree line in sloping country. In favourable situations, as, for instance, on the steep rocky sides of Mount Cope, rabbits occur at higher elevations than usual, but neither rabbits nor wombats are found in the open grasslands. It appears that the main factor which militates against the spread of burrowing animals onto the High Plains proper is deep and persistent snow in winter.

Kangaroos and wallabies have not been seen on the High Plains, even by cattlemen who have known the area for a lifetime, and they are very uncommon even at 4800 ft elevation. Unless some unknown species has become extinct and its disappearance has been forgotten, it appears that before the area was occupied by the white man, grazing by higher animals was an insignificant factor in the development of the vegetation.

(ii) *Insects.*—The large and varied insect population of the High Plains has been very little studied. The best-known species is the Bogong moth (*Agrotis infusa*), which migrates in swarms to the mountains and aestivates there gregariously. It does not breed in the mountains, however, and although its larvae (cutworms) are serious pests in lowland pastures, there is no evidence that it causes damage to alpine grassland (Common 1954). Larvae of scarabs and other beetles are common in the soil, but have not assumed plague proportions even in the years when they caused great damage in lowland pastures.

TABLE 6

CLIMATIC FACTORS AFFECTING GROWTH OF VEGETATION ON THE BOGONG HIGH PLAINS

Favourable	Unfavourable
General thaw in late October to November	General thaw earlier or much later than late October or November
Thaw hastened by rain	Slow thaw induced solely by rising temperatures and not followed by rain
Frosts following the thaw few and light. No late frosts	Thaw followed by many frosts or frosts continuing throughout the season
Weather calm or winds moderate	Strong winds and much windy weather in snow-free period
Regular heavy falls of rain throughout the season, accompanied by moderate to high temperatures	Long dry spells in summer accompanied by either low or very high temperatures

Several species of grasshoppers are extremely abundant in some years and in severely infested areas they shorten the sward considerably. They do not, however, kill the plants as do the larvae of two insect species, a casemoth and a swiftmoth.

(1) *Casemoths.*—A casemoth (*Plutorectis caespitosae* Oke) (Oke 1947; White 1948), the larvae of which feed exclusively on snow grass, is a normal but inconspicuous inhabitant of the grasslands of the alpine areas of Victoria and New South Wales. The larvae feed intermittently, deep in the tussocks, where they chew through the leaf blades just above the sheathing bases. Only a small portion of the blade is eaten, but in heavily infested areas the tussocks are completely cut through at the base and do not recover.

Casemoth damage may be diagnosed by the pellets of excreta, which consist of pieces of grass arranged parallel to one another, with a single piece lying across one end of the bundle. Affected areas also have a characteristic appearance. At first they are roughly circular in outline and the area of dead grass in the centre is surrounded by a narrow zone at the margin where the grass has a yellow, unhealthy appearance. In the centre of the patch the dead grass lies apparently undisturbed, but examination shows that the whole sward is lying loose as if it had been cut by a mower or by shears. The patches enlarge during the summer, and the dead grass turns brown. After it has been covered by a winter's snow it is flattened and bleached and the old cases of the insects become obvious.

(2) *Swiftmoths* (*Hepialidae*).—Collections made in November 1951 by Mr. C. J. R. Johnston of the Victorian Department of Agriculture established the presence within the High Plains area of both larvae and adults of at least one species of *Oncopera.* This genus is included in the Hepialidae (swiftmoths), a family in which the larvae are known to be damaging root-feeders in pasture. Officers of the New South Wales Department of Agriculture have established that *Oncopera alpina* is a very destructive pest of *Poa australis* on Mount Kosciusko.

Patches of grass killed by swiftmoths can be readily distinguished from those killed by casemoths. They do not enlarge during the summer and mechanical damage to the aerial parts of the tussocks is slight. When the dead grass is pulled away, long tubular galleries made of pieces of grass leaves cemented together with silk are found here and there at the bases of the tussocks. The pupal skin of the insect is commonly present at the mouth of the gallery. The galleries lead back to a maze of tunnels in the soil.

The Victorian species have not been identified and the life histories are not known. In other Hepialidae, however, the larvae live for many years in the soil. Usually the first sign of damage is the death of the plants on which the larvae have been feeding. This commonly coincides with, or immediately precedes, the emergence of the adult insects. Mating takes place as soon as the adults emerge. The female lays the eggs immediately after mating and distributes them over an area of at least a few square feet by spraying them forcibly while rotating her abdomen. It is only when egg-laying is completed that the female flies. This means that, once established in an area, hepialid colonies tend to persist and distant new colonies are not readily established.

(3) *The Extent of Insect Damage.*—Since 1944 casemoths have caused serious damage only during the years 1945–1947, and only on grassland A, on soils derived from metamorphic rocks. The affected patches were widely distributed; none was larger than 2 acres, most were much smaller. Similar but much more extensive damage was reported from Mount Kosciusko for the years 1946 to 1948. It appeared that the insect was one which was likely to devastate large areas, but in Victoria its numbers had diminished considerably even in 1947, and since then no extensive damage caused by this insect has been observed. In recent years it has even been difficult to locate single specimens.

Patches of grass killed by swiftmoth larvae were first recognized in 1948, and more than 90 per cent. of the patches of dead grass seen since then have had swiftmoths associated with them. Swiftmoth damage has been recorded in grasslands A, B, and C on both metamorphic and basalt areas, as well as in snow gum woodlands. It has not been observed on snow patches, or in areas in which shrubs are dominant. Swiftmoth patches were numerous throughout the whole area in 1949, 1950, and 1951. Many large areas on the northern grassy slopes of Mount Cope were severely damaged in 1951, and they were much extended in 1952. This was the year in which the damage appeared to reach its maximum. In 1954, areas of grass newly damaged by swiftmoths were small and rare, and none were seen in 1956, 1957, or 1958. From the foregoing it is clear that both the casemoth and the swiftmoth are responsible for spectacular damage to the grass in some seasons, but are inconspicuous in others. As far as we are aware, the swiftmoth is the more widespread and damaging insect.

The underlying causes of severe sporadic damage by these insects are unknown. Casemoth damage followed close on a succession of very dry summers and the affected grassland was usually on north- and west-facing well-drained slopes. In timbered country, swiftmoth damage was widespread and severe in areas which were burnt in 1939. Areas which escaped that particular fire have shown little or no trace of damage. On several areas of the Bundarrah and Bucketty Plain Tops swiftmoth damage was strictly confined to previously burnt country, extending to and ceasing at its junction with unburnt country. Two of the largest patches of swiftmoth damage on the High Plains were on country known for certain to have been burnt, and damage is frequently severe where there are scattered patches of bare ground in otherwise good swards of grass. It is, therefore, a reasonable assumption that degeneration of grassland caused by fire, and possibly by overgrazing, predisposes to attack by swiftmoths. Dick (1940) believes that overgrazing and fire have given rise to conditions in New Zealand tussock grassland which favour attack by the destructive insects such as noctuid moths.

Regeneration of snow grass has generally been successful in the areas where it was killed by insect attack. The process of recovery, however, is slow and areas damaged in 1945 can still be identified by the abundance of herbs and shrubs amongst the grass tussocks. It will be shown that grazing reduces the rate at which grassland recovers from insect damage.

(iii) *Grazing.*—Since shortly after their discovery by white men in 1853, the High Plains have been used for summer grazing. The area has always remained the property of the Crown and is let under grazing licence in "runs" of varying size.

Before 1900 or thereabouts the area was chiefly grazed by horses and cattle, the former being the more numerous. Since then cattle have increased in importance and concurrently the number of horses sent up each year has shown a steady decline, until today only about 50 are grazed on the area. Sheep were not taken up until some time after 1890 and although, until their entry was forbidden in 1947, small flocks were grazed with some regularity on a few runs, large numbers were taken up only in drought years. In the summer of the 1901 drought approximately 100,000 sheep were on the Plains, some coming from as far afield as New South Wales. Similarly, the years 1914, 1926, and 1939 saw heavy grazing of the area by sheep, although the 1901 total has never since been reached. In drought years, too, increased numbers of cattle and horses were brought onto the area, so that the whole tendency in the past was towards severe grazing of the High Plains whenever the nearby lowlands were experiencing dry conditions. It is said that the area was practically eaten out in the 1901 drought, and that this caused the disappearance of a number of herbs which were previously abundant in the sward. The summers of 1914 and 1939 were also notable for heavy grazing of the area.

Over the years the general grazing pressure on the High Plains has steadily increased because of the disappearance of grass from great areas of the surrounding mountain slopes. The forest floor of the woollybutt (*E. delegatensis*) country was formerly predominantly grassy, and this country, together with that occupied by snow gum, was regarded as the choicest of the summer grazing lands. The failure of the woollybutt country to provide grass is a comparatively recent phenomenon, and is due to the fact that it was regularly burnt by the cattleman over a long period of years. The fires were lit in an endeavour to improve the palatability and nutritive qualities of the grass. The earliest fires had the desired effect but resulted in a progressive increase in the amount of scrub (*Eucalyptus* seedlings and shrubs) present. The ultimate result has been that the scrub now dominates these areas to the exclusion of grass. The cattle are, therefore, now concentrated for grazing on the High Plains, and in bad weather find shelter, but little to eat, in the adjacent forests.

The poverty of much of the winter country, which was induced by fire and rabbit infestation, also affected the grazing of the High Plains in so far as it was responsible for lengthening the season during which the high country was grazed. Those run-holders with winter country inadequate for their needs tended to take their cattle to the High Plains as soon as the snow began to melt in spring. The cattle made their way onto higher and higher country as the snow receded. They were left on the area until they were driven off by the snow of the next winter. These practices were not approved by those more fortunately placed for winter feed, nor by the older men whose traditional practice was to restrict the use of the High Plains to that part of the season when flowering was at its peak.

Although what was considered to be the best method of grazing the High Plains was arrived at empirically, it is thought to be sound and has been adopted by those now responsible for the control of grazing in the area. The grazing of sheep is prohibited and that of cattle limited in time and intensity. Cattle are not brought into the area until some weeks after the general thaw and are taken off in early autumn. In addition, a limit is placed on the numbers of cattle allowed to enter. It is to be noted, however, that in at least some recent years the number of cattle actually grazed on the area has been fewer than the maximum set by the Advisory Committee. For instance, it is estimated that in 1949, 7030 head of cattle were grazed on the area. The estimated figure for 1951 is 7110. For both these years the maximum was set at 9000.

(c) *Fire*

Although it was the practice to burn the timbered country to the line marking the upper limit of the woollybutt, the cattlemen never set out to burn the open grasslands. No-one knows why. This attitude to fire, coupled with the fact that over a long period of time the cattlemen regarded the High Plains as their particular province and were recognized locally as being in virtual control of it, has had the interesting result that the area has largely been preserved from fire.

Had sheep been the most important grazing animals on the area, as could have happened if the nearby country had been early developed for sheep rather than for cattle, the High Plains would almost certainly have been regularly burnt to improve the feed for them. Similar country was so treated on the Kosciusko Plateau (Helms 1893; Aust. Acad. Sci. 1957), and in the South Island of New Zealand (Cumberland 1944) to its very great detriment. It is perhaps merely a fortunate accident of history which has preserved the High Plains from such treatment. Small fires have undoubtedly spread onto the plains from the neighbouring slopes at rare intervals during the last 70 or 80 years, as, for instance, in 1926, but these fires were of minor importance. In 1938 few of the snow gum woodlands were fire-damaged. Unfortunately, the catastrophic bushfires of January 1939 spread to the High Plains from the north and killed approximately 80 per cent. of the timber. Undoubtedly large areas of shrub and grassland were then swept by fire. Regeneration of the snow gum from suckershoots and seedlings has been very slow. The cattle do not eat the shoots (as do sheep), but regrowth is hindered by severe insect attack which causes die-back of the branches.

III. The Important Plants of the Grassland: Their Field Behaviour and Reactions to Grazing

(*a*) Poa australis *sp. agg.*

This species exists on the High Plains in a number of varieties, each characteristic of a particular type of site. The distinct nature of these varieties is indicated by the absence of intermediates and has been confirmed by transplant experiments. Pending the completion of a review of the genus *Poa* by Dr. M. E. Phillips and Miss J. Vickery of New South Wales, well-established local names are used for the two major varieties, snow grass and ledge grass. For the others informal names have been devised.

(i) *Varieties with folded, almost cylindrical leaves*

(1) *Snow Grass.*—This is the commonest variety of *Poa* and the most abundant plant on the High Plains. Its light-green leaves are slightly less than 0·5 mm wide and are usually sharp-pointed. Snow grass forms tussocks which are from 3 to 12 in. high. Above 5400 ft, snow grass occurs on well-drained sites of all aspects and is the dominant species in most of the open grasslands. It is usually absent from slopes on which snow lies late and it is poorly developed on steep, rocky slopes where the soil is shallow. It extends into the snow gum woodlands and, where these have not been burnt, is the most abundant plant of the field layer. Below 5400 ft, snow grass is common in the timbered country to the south and east of the High Plains, but is much less plentiful than ledge grass in the north (e.g. in the Kiewa Valley).

Snow grass is not rhizomatous and lateral extension of established tussocks is slow. In most years viable seed is produced and seedlings may be found in great numbers in autumn (late March and April) and in spring. Although the seed germinates readily in the field, seedling mortality is very high. Seedlings which occur on bare ground die because repeated frost-heaving prevents establishment of the root system. In poorly drained situations seedlings are killed by submergence. Those which occur around the bases (and in the shelter of the overhanging leaves) of established tussocks also fail to survive because the surface soil dries out in summer.

Seeds of snow grass germinate also under shrubs, but establishment only occurs in the centres of shrubs entering the degenerate phase of their life cycle. The young snow grass plants persist in an attenuated state until the shrub canopy develops a definite gap. As the gap increases in size the snow grass plants grow into normal, dense tussocks. Snow grass will not colonize artificial gaps in shrubs damaged during the building and early mature stages of their life cycle.

(2) *Big Horny Grass*.—This variety is much more robust than snow grass. It has coarse, dark green leaf blades, 6–12 in. long and 1·5–2 mm wide. They are readily damaged by trampling. They are somewhat glossy on the outer (lower) surface and glaucous on the inner (folded) surface. Big horny grass grows in the deep peaty soils of soaks and at the edges of mossbeds, often with *Hypolaena lateriflora*.

(3) *Small Horny Grass*.—The tussocks are smaller and more rigid than those of big horny grass. They vary in height from 1½ to 5 in. The leaf blades are intermediate in colour between the light green of snow grass and the dark green of big horny grass, and are also intermediate in diameter. The variety occurs in situations which appear to offer less favourable conditions than those required by snow grass. Flat areas with shallow topsoil and which are alternately very wet and very dry support a sparse growth of this variety. It is also common on mountain tops and on exposed slopes at elevations of 6000 ft and upwards. It occurs with snow grass in grassland C.

(4) *Blue* Poa.—It is probable that two forms, neither of which is common, are included in this category. One appears to be a glaucous soft form of snow grass and the other a glaucous form of big horny grass.

The varieties (2), (3), and (4) produce viable seed, but there are as yet no certain records of seedling establishment for any of them.

(ii) *Varieties with broad flat leaves*

(5) *Ledge Grass*.—This variety is the only one of group (ii) which occurs on the High Plains proper. Unlike the varieties (1)–(4), it is weakly rhizomatous and has annual leaves. The leaves of the current season's growth are underlain by a mat of dead leaves from earlier seasons. The leaf blades are about ¼ in. broad (sometimes more) and vary in length from about 2 in. to more than a foot. They are flat and taper abruptly to a boat-shaped tip. The sheaths are flattened and are usually purple.

The distribution of the variety within the area is peculiar. It is abundant in the woollybutt forests of the Kiewa Valley but does not extend into the forests to the south and west. On the High Plains it grows only on well-drained sites below 6000 ft and reaches its greatest development in shrub communities. It is sometimes present in snow gum woodlands, particularly where they occur on sloping rocky sites and have a discontinuous understorey of shrubs. It is also found associated with *Carex hebes* on snow patches and it becomes abundant on these areas if they are protected from grazing.

Ledge grass develops well only where there is shelter from the prevailing wind. In exposed situations its leaves are pale green, short, and folded, and have dead tips. In sheltered places, the leaves are long, dark green, and expanded. Ledge grass is able to spread slowly by vegetative means into areas occupied by *Carex hebes* or by low shrubs, but it will not normally invade bare ground. As with snow grass, regeneration by seed is successful only when the seedlings are associated with shrubs. Ledge grass will occupy the central gaps of degenerate shrubs in both tall and low shrub communities but, in addition, it is capable of invading low shrub communities long before they reach the degenerate phase. Once established, its leaves project beyond the shrub canopy. Any gaps in the canopy which appear, due to accident, during the building and mature phases, are likely to be exploited by ledge grass.

Many of the shrub communities in which ledge grass is now abundant have developed in place of tussock grassland in which snow grass was dominant. The evidence suggests that, although ledge grass occupies gaps in the shrubs, it will eventually be replaced by snow grass when the shrubs degenerate and are suppressed.

(6) Poa australis *var.* latifolia *Benth.*—According to Dr. M. E. Phillips, this name should be assigned to another variety with flat leaves which occurs in gullies and soaks in the steep country surrounding the plains. It is larger and coarser than ledge grass, but otherwise can only be distinguished by the fact that the leaf blades of ledge grass have parallel margins for most of their length, while those of variety (6) taper to a long point.

(*b*) Carex hebes

This species is a rhizomatous perennial, the roots of which penetrate to a depth of at least 3 ft. The root system is dense and fibrous, and occupies the soil thoroughly from the surface to a depth of 12–18 in. The rhizome occurs at a depth of $\frac{1}{2}$–1 in. but on eroded ground may be on the surface of the soil or just below it. The leaves are usually from 2 to 5 in. long, but in favourable situations may be 9 in. long.

The species occurs in all the communities of the High Plains except those of the mossbeds. It reaches its greatest development in the vegetation of the snow patches, where it is the most abundant species. It is conspicuous in grassland or shrub communities only when these have been moderately damaged. Between the tussocks in grasslands B and B_1 there are many flat depressions on which *Carex hebes* is dominant. It tends to become abundant on areas in which snow grass has been killed by insects. Where the dead grass is removed, the soil is laid bare and tends to remain so. Where the dead grass is undisturbed, scrambling herbs such as *Asperula* fix the litter to the soil and allow recolonization by the grass. Where the dead grass has been moderately disturbed, *Carex* commonly takes over. In a sward which is recovering from damage it is common to find plants growing on three levels. On the lowest there are the colonists of bare ground, and on the highest level there is snow grass and the herbs associated with it. *Carex* occupies the intermediate level.

Carex hebes also tends to become prominent in places where scattered snow gums have been killed by fire. Under unburnt trees snow grass extends right up to and surrounds the base of the trunk, but where the crowns of trees have been burnt *Carex hebes* sometimes forms a close turf on the ground covered by the original tree canopy. It appears that the heat from the crown fire was sufficient to kill the original grass and to scorch the surface of the litter. *Carex hebes* then became prominent and has persisted. (Plate 5, Fig. 4.)

Carex is heavily grazed, and grazing encourages the establishment of a turf and prevents the accumulation of litter. The soil becomes thoroughly permeated by the fine roots of *Carex* and does not absorb water as readily as does soil under snow grass.* Water tends to lie in *Carex*-covered depressions in swards of *Poa* and this, coupled with close grazing, inhibits succession to a snow grass community.

Carex produces an abundance of ostensibly fertile seed, but we have not observed seedling development in the field, nor have we yet been able to germinate seed in the laboratory. *Carex* persists and spreads by vegetative means, but is only a feeble colonist of bare ground. However, it will slowly colonize the ground under shrubs.

(*c*) *Herbs*

All except very few of the herbs are perennial. They flower and fruit freely in most seasons, but on the whole seedling establishment is rare. Most species are rhizomatous or stoloniferous and spread chiefly by vegetative means. The important species will be fully discussed in paper II of this series.

(*d*) *The Pattern of Grazing*

Ledge grass, *Carex hebes*, and the inflorescences of all *Poa* varieties are highly palatable to cattle. They also eat the mature leaves of snow grass growing in sheltered situations (e.g. in the woollybutt forests). On the plains, however, although snow grass and the horny and blue varieties of *Poa* appear capable of providing an immense amount of herbage for grazing, this impression is misleading. The mature fibrous leaves of these varieties are normally avoided by stock. New leaves occur mixed with living and dead leaves of previous seasons; they are not readily severed or pulled away from the sheath. It is only when new shoots appear on burnt tussocks that a fresh green "pick" is available. The commonest result when an animal attempts to graze these varieties of *Poa* is that portion of the tussock is pulled out. The shoots come away with the bases surrounded by dead leaf-sheaths which are not eaten. In some years, particularly those in which the growth of herbs is limited by dry conditions, the grassy areas of the High Plains are littered with innumerable loose pieces of tussock which have been pulled out by cattle; the damage to the sward is obviously considerable.

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* Mean time (min) for infiltration of ½ in. water, six sites: snow grass, 21; *Carex hebes*, 73.

The peak of flowering in *Poa* is usually in mid January, and in seasons when the grasses flower profusely the cattle gain condition rapidly as they graze on the inflorescences of *Poa* and of the herbs. During this period, in good seasons, there is only limited grazing of the vegetative parts of the herbs or of snow grass, and few shoots of *Poa* are pulled out. The leaves, as well as the inflorescences, of ledge grass are eaten. Meanwhile the vegetation of the snow patches tends to be neglected, but may be grazed later in the season. The leaves of herbs are grazed early and late in the year, and at these times there is a good deal of uprooting of *Poa* shoots.

In poor seasons, when *Poa* does not flower well, the herbs of grassland C and patches of herbs in other communities are grazed almost to ground level. Ledge grass is heavily grazed and the shoots of other varieties of *Poa* are pulled out. The more unfavourable the season, the more heavily are the snow patches grazed. In poor seasons, too, the *Carex* species of the mossbeds (chiefly *C. gaudichaudiana*) are heavily grazed. Cattle visit mossbeds for water, but in good seasons they neglect the usually sparse growth of sedges. However, in places where *C. gaudichaudiana* grows thickly on recent deposits of raw silt and other debris it is grazed closely every year. Shrubs and snow gum shoots are not grazed by cattle under any normal circumstances.

IV. The Grassland Communities

The grasslands cover an area of considerable geological diversity. Older Basalt, granitic, and a variety of metamorphic rocks occur. This diversity of parent material is not reflected to a great extent in the soils, for in all well-drained situations soils which can be referred to as alpine humus soils have developed. These are of the type described from the Kosciusko Plateau by Costin, Hallsworth, and Woof (1952). The soil type occurs in both deep and shallow phases. The shallow phase in its more extreme forms can be included in the group described for Victoria (Leeper 1957) as brown soils.

Many of the areas occupied by grasslands are below the general tree line for the region. Although the grassland continues, with very little alteration, as the field layer of open snow gum woodland, there is no evidence, either from plant remains or in the written or remembered record (Skene and Smyth 1874), to suggest that the open grassland formerly carried trees. A similar occurrence of low level alpine grasslands in the Snowy Mountains of New South Wales has been ascribed to frost hollow effects (cold-air drainage) (Costin 1954). For Victoria, at least, this hypothesis remains untested.

The most widespread type of vegetation on the High Plains is low-tussock grassland, in which one or other of the varieties of *Poa australis* is dominant. The grasslands are of several kinds and they grade into one another as well as into the shrub communities.

One of the objects of this work has been to establish the nature, origin, and development of the alpine grasslands, and with this in view we have distinguished four major types, as follows:

Grassland A	Closed tussock grassland,
Grassland B	Open tussock grassland,
Grassland B_1	Open tussock grassland with shrubs,
Grassland C	Open tussock grassland, rich in herbs,
Grassland D	*Carex* grassland (snow patch vegetation).

(*a*) *Grassland A* (Plate 4, Fig. 1)

Grassland A is the most nearly natural community of the area. It appears to be comparatively stable under the present climatic conditions and grazing incidence. Grazed areas under observation since 1941 have shown no significant change.

This is a closed community dominated by snow grass. On casual inspection the community appears to be a vigorous, pure stand of the grass but, in all examples we have studied, about 40 species are present. Most of these are perennial herbs (Table 7) and the most constant are *Asperula gunnii*, *Carex breviculmis*, and *Microseris scapigera*. *Celmisia longifolia* is occasional to rare.

Ledge grass and five grass species of genera other than *Poa* are occasional. These grasses and the remaining herbs are so scattered that they contribute little to the structure of the community. Shrubs are of still less importance. Seven species have been recorded as constant in the sward, but the individual plants are spindly and suppressed.

Two typical areas have been sampled by the point quadrat method (Table 7; see also paper II of this series). Both are situated in the head of the Scout Hut Branch of Middle Creek. Site 1 is just below Cope Hut and site 2 on the northern side of the valley just above the Scout Hut (Fig. 1, sites 5 and 6 respectively). In both examples the vegetative cover is almost complete and bare ground occupies at the most 2 per cent. of the area.

Snow grass occurs in large tussocks which are as much as 2 ft in diameter and up to 12 in. high (exclusive of inflorescences). The sward is underlain by a dense mass of grass leaves and litter which, in the finest examples of grassland A, may reach a thickness of 4 in. In most cases it is between 2 and 3 in. thick. It carpets the spaces between the tussocks, but is not visible from above the sward because the spaces are over-arched by the spreading, very numerous leaves of the grass. Snow grass occupies more than 90 per cent. of the area and makes up 93 per cent. of the sward.

Most of the herbs, shrubs, and other grasses are rooted in the spaces between the tussocks. They, therefore, grow in dense shade. The shrubs are dwarfed, and of the herbaceous plants only *Microseris*, with its long scape and prominent capitulum, and *Asperula*, which straggles over the tussocks, are obvious from above. It can be seen from Table 7 that these two species, together with *Carex breviculmis*, give comparatively high figures for percentage overlapping cover and are the only species other than snow grass which make a substantial individual contribution to the sward. Even so, the species other than *Poa* collectively make up less than 8 per cent. of the sward.

Grassland A is found on gentle slopes of all aspects where there is some shelter from the wind. It occurs only on soils with a very deep A horizon (up to 18 in.), in places where drainage is good but moisture is abundant. At present the community does not cover large areas (the examples we studied are between 1 and 2 acres in extent), but it occurs with a patchy distribution throughout the whole area.

TABLE 7

GRASSLAND A: DATA FROM POINT ANALYSIS, 1948

Species	Percentage Overlap Cover		Percentage in Sward	
	Site 1	Site 2	Site 1	Site 2
Poa australis var. snow grass	93	91	93	92
Total shrubs	—	—	0·9	0·5
Total herbs*	—	—	5·7	7·5
Bare ground + litter	1·3	0·6		
7 shrub species, each	<1·5		<0·2	
6 shrub species, each		<1·2		<0·2
Herbs:				
Asperula gunnii	15·0	17·0	3·0	3·2
Carex breviculmis	8·0	7·5	1·5	7·1
Microseris scapigera	4·0	4·0	0·4	0·5
Trisetum spicatum	0·3	3·3	0·03	0·2
Ranunculus lappaceus	0·3	2·1	0·02	0·3
Carex hebes	0·2	1·6	0·01	0·2
Rumex acetosella	0·1	1·4	0·01	0·2
Scleranthus biflorus	—	2·1	—	1·0
Agropyron velutinum	—	1·4	—	0·2
Brachycome decipiens	0·4	1·7	0·03	0·1
Stipa nivicola	1·0	—	0·3	—
6 herb species, each	<1·0		<0·08	
11 herb species, each		<0·7		<0·07
Number of species (1000 points)	23	28		
Total number of species present	39	40		

* Including grasses other than *Poa*.

(*b*) *Grassland B* (Plate 4, Fig. 2)

This community is clearly derived from grassland A after severe damage by fire, insects, or grazing. Snow grass is the dominant species, but the tussocks are smaller than in grassland A. The sward is from 5 to 8 in. deep and overlies a litter layer which varies from ½ in. to 2 in. in thickness. Ledge grass is rare in the community. In grassland B the continuity of the sward is interrupted and, in the spaces between the tussocks, herbs, particularly *Senecio lautus*, *Microseris scapigera*, *Rumex acetosella*, *Ranunculus lappaceus*, *Plantago tasmanica*, *Asperula gunnii*, *Carex breviculmis*, and *C. hebes*, are abundant. There is little bare ground and shrubs are rare and small.

Grassland B_1 (Plate 5, Fig. 1).—In this category we include what may be two distinct communities. Snow grass is the dominant in one and ledge grass in the other. However, because grassland B_1 (snow grass dominant) includes variable amounts of ledge grass, and vice versa, and also because the two communities both show severe patchy soil erosion, we classify them together. Both grade into pure shrub communities.

Grassland B_1 (snow grass dominant) closely resembles grassland B, but includes large scattered patches of bare ground. The herbs normal to grassland A are present, but are not abundant. Shrubs, chiefly *Hovea longifolia*, *Grevillea australis*, *Prostanthera cuneata*, and *Phebalium podocarpoides*, occur between the tussocks and around the edges of bare ground. The factor which initiated the erosion is not always apparent, but some of the bare ground is the result of severe burning at some time in the past.

Grassland B_1 (ledge grass dominant) includes the shrub species which are common in grassland B_1 (snow grass dominant), but some species which are uncommon in the latter community also occur. These are *Bossiaea foliosa* and *Orites lancifolia*. The community usually occurs in open spaces in snow gum woodlands, and there is abundant evidence that the immediate chief cause of soil erosion is the damage suffered in the 1939 fires.

(*c*) *Grassland C* (Plate 1, Fig. 1; Plate 5, Fig. 2)

This widespread community is characterized by its patchiness, the abundance of perennial herbs, and a very poor development of shrubs. The tussocks of *Poa* are from 2 to 4 in. high and are chiefly of snow grass, with the small horny variety locally abundant in the flatter, wetter areas. *Poa* does not form a uniform sward, but occurs in patches, sometimes a foot, sometimes many yards across. The community is very rich in herbs, all of which, with the exception of *Leptorrhynchus squamatus*, may be found in grassland A. They occur chiefly in the shallow depressions between the patches of grass. When in flower in early summer they give a characteristic and colourful appearance to the community. The species present vary with the locality. In Pretty Valley the most abundant are *Leptorrhynchus*, *Senecio lautus*, *Asperula gunnii*, and *Carex breviculmis*. The grass *Agrostis venusta* is also common. On the slopes of Mount Nelse, similar grassland is rich in *Celmisia longifolia*. *Leptorrhynchus* was very rare in the Mount Nelse area before 1945, but is now fairly plentiful. On the spurs of Mount Fainter and locally elsewhere, *Rumex acetosella* is the dominant herb. On the areas of Older Basalt in the head of Pretty Valley and around the head of the Bundarrah River, *Ewartia nubigena* and species of *Gnaphalium* are frequent in the community. So is the dwarf shrub *Pentachondra pumila*. Around soaks and in damp places in this area *Claytonia australasica* may occur in large patches.

Poa is much less abundant than in grasslands A and B. In extreme examples the vegetation scarcely merits the name "grassland", as the herbs are much more abundant than the grass. The community is remarkable for its variability. It shows great variations, even in the space of a few yards, in the species present, in the amounts in which they occur, and in the numbers and size of the patches of bare ground. Some of these variations are illustrated by the data of Table 8, in which a comparison of three areas of grassland C is made. (See also paper II, Plates 1–3). For further comparison a similar analysis of grassland type A is given.

TABLE 8

GRASSLANDS C COMPARED WITH A

	Type A	Type C		
		(1)	(2)	(3)
A. Percentage composition of the sward as measured by point analysis				
Species:				
Poa	98	67	43	32
Shrubs	0·2	4	0·3	0·6
Herbs	1·2	29	57	67
B. Percentage cover (Poa *and bare ground*)				
Poa	90	70	43	32
Bare ground	1	2	6	12
C. Number of species present				
No. of spp.	28	31	26	22

With increasing erosion (going from left to right), note:
(*a*) the replacement of *Poa* in the sward by herbs,
(*b*) the eventual diminution of the total number of species,
(*c*) the increase in bare ground and smaller coverage by *Poa*.

Grassland C is widespread on all the gentle slopes of Pretty Valley (Fig. 1) and on the lower slopes of Mount Nelse. It is not, however, confined to these areas, as it occurs in Rocky Valley and elsewhere. It cannot be sharply delimited from the other grassland communities, and on Mount Nelse it grades into a herb field community in which *Celmisia longifolia* is more abundant than *Poa*. Locally, it grades into the shrub communities which occur at the edges of mossbeds. The general distribution of grassland C (including the absence of trees) cannot simply be related to cold-air drainage, because the community occurs more or less uniformly on long, smooth slopes as well as on flat or gently sloping country. Neither can the occurrence of grassland C be accounted for on the basis of soil type except that, in general, the A horizons of its soils have a lower content of organic matter and are shallower than those of the soils which support grasslands A and B.

It is probable that lack of shelter from strong winds (chiefly the prevailing wind) is the important factor in determining the occurrence of this community.

(*d*) *Grassland D* (Plate 5, Fig. 3)

This community is recognized by the dominance of *Carex hebes*, which forms a thin, fairly uniform turf. *Poa australis* (ledge grass), *Danthonia nudiflora*, and *Trisetum spicatum* also occur, together with a great variety of herbs. Small shrubs, although inconspicuous, are always present. Grassland D is found on all but the steepest and most sheltered of the snow patches, i.e. areas usually with a southerly or easterly aspect on which the snow persists beyond the general thaw.

V. Acknowledgments

For support of the work described in this and succeeding papers of the series we are indebted to the State Electricity Commission of Victoria. We have been assisted in many ways by officers of the Commission, and we thank them for their courtesy and friendly cooperation. We especially thank Mr. L. T. Guy, sometime Construction Engineer, Kiewa Hydroelectric Scheme, Mr. H. H. C. Williams, Construction Engineer, Kiewa Hydroelectric Scheme, Mr. C. B. Kay, Chief Forestry Officer, S.E.C., Mr. W. T. Feagan, Works Forestry Officer, Kiewa Hydroelectric Scheme, Mr. M. F. Romuld, sometime Officer-in-Charge, Meteorological Station, Bogong High Plains. We are grateful for permission to use the meteorological data and the information embodied in the map, which was drawn by Miss J. J. Wood.

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One of us (S.G.M.C.) has been greatly assisted by many of the cattlemen, both in discussion of the history and problems of the area and in such practical matters as generous hospitality and transport to and from and within the area. It is a pleasure to mention especially Mr. M. F. MacNamara of Cobungra, Mr. Brendon Fitzgerald and the late Mr. George Fitzgerald of Shannonvale, and Mr. H. H. Fitzgerald of Omeo.

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ECOLOGY OF BOGONG HIGH PLAINS. I

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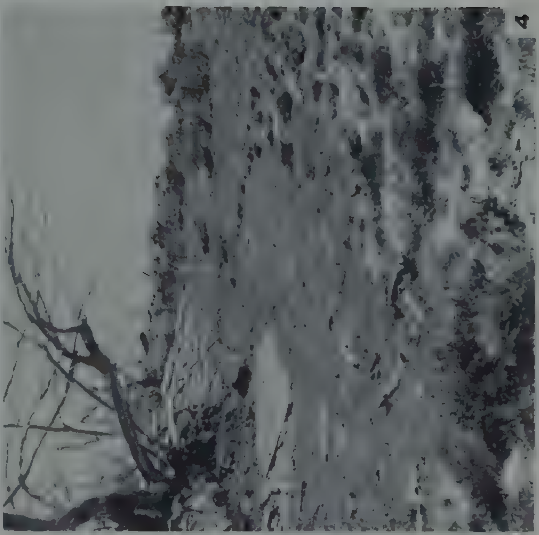

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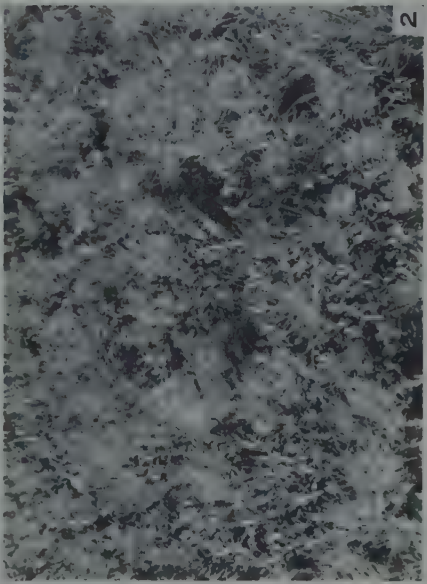

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Explanation of Plates 1–5

Plate 1

Fig. 1.—General view of Bogong High Plains. Mount Nelse (6175 ft) is in the background, an area of grassland C in the foreground.

Fig. 2.—General view of Bogong High Plains, with Mount Cope (6024 ft) in the background. The plant communities are: foreground, low shrub community; centre left and Mount Cope, snow gum woodland; centre right, grassland C with mossbed. Photograph by courtesy of the late Dr. L. Ellison.

Plate 2

Fig. 1.—*Poa* grassland A (snow grass) extending right to the base of the trunks of unburnt snow gum at the edge of woodland.

Fig. 2.—Mossbed. Stream meandering on peaty alluvium, Pretty Valley. The steep banks in the middle distance have formed along cattle tracks.

Plate 3

Fig. 1.—Snow gum woodland (1951) killed by fire in 1939; note scrub beneath standing dead timber.

Fig. 2.—Snow patch, showing severe accelerated erosion, Mount Hotham.

Fig. 3.—Accelerated erosion on site of snow patch and former mossbed (left-hand bottom corner). Note cattle tracks.

Fig. 4.—Erosion on mountain top, Mount Hotham. The tussocks of snow grass are widely scattered, with bare soil and stones between.

Plate 4

Fig. 1.—Grassland A, snow grass tussock undamaged under unburnt fence built of dead snow gum.

Fig. 2.—In foreground, eroded mossbed. Behind this an area of grassland B. An old cattle track crosses the boundary between the two, and here wind scooping has removed the soil from between the grass tussocks.

Plate 5

Fig. 1.—Grassland B_1, Rocky Valley, 1949. Scattered tussocks of snow grass with bare ground between, partly colonized by shrubs. Note remnants of snow gum burnt in 1939. The lower half of this photograph would serve also as an illustration of grassland B.

Fig. 2.—Grassland C, Pretty Valley. This illustrates one of the least damaged examples of this community. The plants are *Poa* (snow grass) and the herb *Leptorrhynchus*.

Fig. 3.—Grassland D. Snow patch with *Carex hebes* dominant. Mossbed in background.

Fig. 4.—Edge of snow gum woodland burnt in 1939, photographed 1950. Note heavily grazed turf of *Carex hebes* under former tree canopy.

THE ECOLOGY OF THE BOGONG HIGH PLAINS

II. FENCING EXPERIMENTS IN GRASSLAND C

By Stella G. M. Carr* and J. S. Turner†

[*Manuscript received December* 23, 1958]

Contents

		Page
	Summary	34
I.	Introduction	35
II.	Methods	35
	(*a*) Point analysis of the vegetation	35
	(*b*) Soils	37
III.	The effects of the exclusion of grazing in grassland C	38
	(*a*) Results of experiment	39
	(i) General observations	39
	(ii) Luxuriance	40
	(iii) Percentage overlapping cover	41
	(iv) Composition of the sward	50
	(v) Soils	53
	(*b*) General conclusions	54
IV.	The status of grassland C, with special reference to erosion	56
	(*a*) Erosion	56
	(*b*) The derivation of the community	58
V.	Catchment management on the High Plains	60
VI.	Acknowledgments	60
VII.	References	61

Summary

A 10-year fencing experiment in the eroded grassland, type C, of the Bogong High Plains has established the value of the point analysis method for the quantitative study of continuing change in vegetation. The results show that the exclusion of cattle from this widespread type of subalpine grassland results in a gradual improvement in the amount of vegetative cover, especially in that provided by the herb *Celmisia*. Over the 10-year period there have been striking soil changes in the fenced plot, resulting in an increase in organic matter and in field capacity, and a significant decrease in bulk density. These findings enable one to make recommendations on catchment management in this area. They have also led to the hypothesis that the eroded grassland has been derived from a herb-field similar to that still existing in the higher parts of the area.

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I. INTRODUCTION

The plant communities of the High Plains form a complex intergrading series, and appear to reflect even small differences of aspect, exposure, and drainage with remarkable subtlety and fidelity. The vegetation has been grossly disturbed by two factors—fire and grazing, the incidence of which have greatly increased over the last 100 years. The object of the experiments to be described was partly to determine the status of the various communities, and partly to investigate the effects of cattle grazing. It was beyond our resources to set up any trial plots other than those involving the presence or absence of grazing, and all experiments consisted of a quantitative study of comparable fenced and unfenced plots with the object of testing a hypothesis that a continuation of cattle grazing prevents or delays the development of a complete cover of vegetation.

As it has never been the custom in this region to fence individual cattle runs, it is impossible to compare land leased by men with different ideas of the management of alpine pastures. However, some information has been gained from one freehold paddock at an altitude of 4800 ft, which has been fenced for many years and grazed only lightly and intermittently. The experimental data have also been supplemented by annual reconnaissance, and the study of small permanent quadrats and of old stockyards used for holding cattle (or sheep) for short periods. Valuable information has also been supplied by graziers who have known the Plains over a lifetime.

II. METHODS

(a) *Point Analysis of the Vegetation*

After trials of various well-known methods and some years' experience of point analysis in subalpine pastures at Omeo (S.G.M.C.), this method was adopted as a suitable means of analysing complex grassland and for recording changes over a long period. Experience over 12 years has strengthened our view that point analysis is a most valuable quantitative ecological method.

In 1945, following Levy (1933) we used single pins, distributed at random over the plots. For plots of the sizes to be specified, we used 1000 point samples. In 1946 and later years, the pins were held in rows of 10, each 4 in. from its neighbour, in steel racks, the 1000 samples being obtained in 100 randomly placed groups of 10. In 1946 we checked the reliability of the method by using, successively, sampling numbers from 250 to 2000 in sets of 250. For each set the whole plot was sampled. The results obtained showed that for our purposes a sufficiently small variance was obtained by the use of 1000 samples. In later years, whenever time allowed, each plot was sampled twice, 1000 points in racks of 10 being used. The two estimates are shown on some of the graphs.

In 1949, Dr. D. W. Goodall, then a senior member of our field parties, began a critical study of the point quadrat method, the results of which have been published elsewhere (Goodall 1952). He showed that for five species taken together about 700 single points give the same precision in estimating *percentage overlap cover* and *contribution to sward* as do 2000 points taken in groups of 10. We, therefore, abandoned the use of racks and reduced the number of point samples to

600–700 for each plot. Goodall also showed that successive observations at the same series of points give a more precise estimate of change than is possible by the use of random sampling. In the later years of the experiment, therefore, all point samples were taken at the intersections of the lines on a rectangular grid superimposed over the whole plot. In the years in which we introduced modifications of the general method, any possibility that these might be responsible for variability of the results was guarded against by sampling the plots by both new and old methods. Throughout the whole series of experiments the size of pin used has remained the same (4 mm diameter). Special details of procedure are set out below:

(1) In most years since 1945, working parties of 12–20 graduates spent 2–3 weeks on the plains in January. Each plot was sampled by a team of 9–12 workers.

(2) In order to maintain uniformity of procedure and a high standard of accuracy, the teams of observers and recorders were selected so as to contain at least one observer with previous experience. New members were trained and used first as recorders. As far as possible windy and wet days were avoided for sampling. The pins, whether in racks or single, were held firmly in a vertical position with one end in or on the ground. The contacts made by the pin were reported by an observer to a recorder. Both workers disturbed the vegetation as little as possible. As far as possible the data were analysed during the expedition. This allowed a check of any result which appeared anomalous and the detailed investigation of areas showing changes. The tedious analysis of large numbers of point quadrat samples was shared by the whole team.

(3) All loose plant material was recorded as litter. Dead *Poa* leaves were counted when they were still firmly attached to the tussock but obviously dead. Care was necessary to distinguish leaves which were dead at the tip but living at the base. In the analysis of results for grassland C the data available for "dead *Poa*" have not been used, but are of importance in the analysis for grasslands B and B_1 (paper III).

(4) Bare ground or rock was recorded only if a sample pin touched no plant part and no litter. Such figures may, however, be misleading, especially in the comparison of different types of community. For instance (Table 1, paper I), the figures for bare ground in grassland A and grassland C are 1 per cent. and 2 per cent. respectively. In grassland A, however, the tussocks are large and form an almost closed stand, and the ground around the bases of the tussocks, and between them, is covered by a thick layer of dead leaves. The soil is thus effectively protected from erosion by wind and water. In grassland C the basal area of the tussocks is small, the grass leaves short and rather sparse. Many of the leaves project over bare ground, so that in many samples the vertically placed sampling pins touched bare ground after hitting vegetation. In this type of community the soil surface is more exposed and much more liable to erode than is indicated by the figure given for absolutely bare ground or by a comparison of the percentages for bare ground in grasslands A and C.

In the later years of the experiment, therefore, data were obtained for both bare ground and bare ground vertically under vegetation. In grassland C the figures for the latter may reach 20 per cent. (see Fig. 2).

(5) The problem of counting contacts in dense tussocks confronted us in dealing with *Poa australis*. We adopted the convention of counting only as far as 10 contacts for snow grass and recording 11 or more contacts as X. For ledge grass we counted up to 8 contacts and called 9 or more X_1. In the analysis of the data X was given a value of 18 and $X_1 = 12$. The method of calculation of these values is set out by Goodall (1953).

(6) The results of the analysis are expressed in the following ways:

(*a*) The percentage of the area which is occupied by each species (percentage overlapping cover)

$$= \frac{\text{The number of samples in which the species occurs}}{\text{Total number of samples}} \times \frac{100}{1}.$$

(*b*) The proportion of each species in the vegetation as a whole (percentage of sward)

$$= \frac{\text{Total number of ``hits'' for each species}}{\text{Total number of ``hits'' on all species}} \times \frac{100}{1}.$$

(*c*) Total luxuriance

$$= \frac{\text{Total number of ``hits'' on all species}}{\text{Number of samples which include living vegetation}}.$$

This figure gives the mean number of "hits" per sample.

(*d*) Luxuriance of an individual species

$$= \frac{\text{Total number of ``hits'' on the species}}{\text{Number of samples in which the species occurred}}.$$

(*e*) Luxuriance of a particular type of plant, e.g. herbs

$$= \frac{\text{Total number of ``hits'' on herbs}}{\text{Number of samples which include herbs}}.$$

(*b*) *Soils*

(i) *Soil Moisture and Organic Matter* (Table 2)

Each plot in grassland C was divided longitudinally by a line beginning 2 yd in from the boundaries at each end. Soil samples were taken at 10 equal intervals along each line. The vegetation and undecayed litter were removed at each site and samples taken to a depth of 3 in. with a 3-in. auger; each was immediately placed in an impervious container.

(1) *Moisture Content.*—About 10 g of soil was dried to constant weight at 105°C and moisture content expressed as a percentage of the oven-dry weight.

(2) *Permanent Wilting Percentage.*—The air-dry soils were sieved to 2 mm, and the coarser particles discarded. After 7 days in the pressure membrane apparatus of Richards and Weaver (1943) the moisture content was determined and expressed as a percentage of the oven-dry weight.

(3) *Field Capacity.*—An approximate estimate of this was made by the determination of moisture content at the sticky point (Piper 1947). In later sampling, field capacity was determined by subjecting the soils to a tension of 100 cm water (Leeper 1957).

(4) *Organic Matter.*—A modification of the method described and reviewed by Walkley (1947) was used. All gross plant residues were discarded and the soils were then ground to pass a 0·5 mm sieve. Duplicate samples of 0·5 g were accurately weighed into small Erlenmeyer flasks. Ten ml of N (1·000) potassium dichromate was added to each, followed by 20 ml of concentrated sulphuric acid. The acid was added quickly to ensure maximum heating. The mixture was well shaken for about 1 min and then allowed to stand for about 30 min. The supernatant liquid was then decanted into a large beaker, leaving behind as much of the soil as possible. The volume of the liquid was made up to approximately 300 ml with tap-water. The whole was titrated with N ferrous sulphate dissolved in N sulphuric acid. Barium diphenylamine sulphonate was used as the indicator, and before titration 10 ml of M phosphoric acid was added to give a sharp end-point. The ferrous sulphate solution was standardized before each day's work.

It was assumed: (*a*) that the carbon made up 58 per cent. of the organic matter of the soil; (*b*) that a recovery of 80 per cent. was obtained.

(5) *Soil Colour.*—The colours of the soils were matched against the standard colours given by the Munsell Color Company Inc. (1941).

(ii) *Bulk Density*

(1) (1957) The mid-line of each plot was divided into four. Sets of samples were taken at the quarter, half-way, and three-quarter marks. The mid-lines of each plot were extended uphill and further sets of samples taken at a distance of 10 yd from the plot boundaries. Two other sets were taken on the north side of the fenced area on a line running parallel with the mid-line of the plot. As far as possible, the samples taken at each point were representative of the major types of cover. At each site the vegetation and any undecayed litter were removed and soil samples were obtained with a 3-in. auger to a depth of 3 in. The volume of the hole left after removal of the sample was measured by filling it with fine sand contained in a measuring cylinder.

$$\text{Bulk density} = \frac{\text{Oven-dry weight of sample}}{\text{Volume occupied by sample in the field}} \times \frac{100}{1}.$$

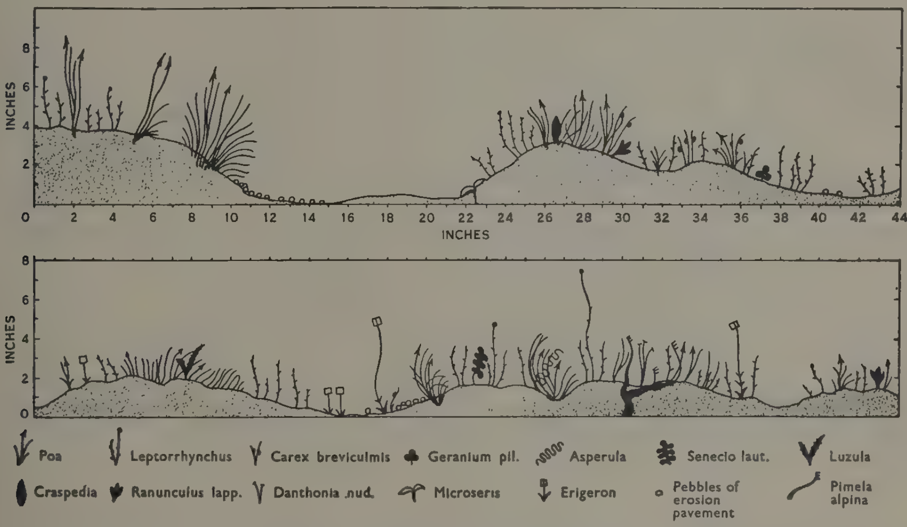
(2) (1958) Samples were also taken in the field in tubes of 2-in. diameter and 3-in. depth. These were matched pairs obtained at regular intervals close to the contiguous (inner) boundaries of the two plots. Bulk density and field capacity were determined as above.

III. The Effects of the Exclusion of Grazing in Grassland C

The area of typical grassland C selected for experiment is at 5600 ft, situated on a gently sloping saddle between two tree-clad, rocky outcrops (Fig. 1 of paper I).

It is about ¼ mile from some rocks at which cattle are regularly given salt, and close to one of the main cattle pads leading from Pretty Valley to Wallace's Hut. It was selected as an area which has for many years been grazed in a way normal for this community.

A rectangular area of fairly uniform vegetation, soil, and slope was pegged out. It was divided into two equal rectangles running up and down the slope, each about 30 by 180 ft. Late in 1946, one rectangle was fenced to exclude cattle; the other served as a control. The choice of which half was to be fenced was made on the toss of a coin. The whole of each rectangle has been analysed by point samples since January 1947. The results are shown in Figures 2–6.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Luzula
Craspedia
Ranunculus lapp.
Danthonia nud.
Microseris
Erigeron
Pebbles of erosion pavement
Pimela alpina

Fig. 1.—Grassland C. Diagram of typical line transects drawn to scale, showing eroded surface and diversity of vegetation.

A list of the major species on the plots is given in Appendix I. A description of grassland C will be found in paper I and this is supplemented best by Plates 1 and 2, illustrating different stages of erosion, and by the diagram of a line transect in Figure 1.

(a) *Results of Experiment*

(i) *General Observations*

The area occupied by bare ground and litter has diminished in the fenced plot from 10·2 per cent. (1947) to 2·7 per cent. (1958) (Fig. 4). The largest response was shown in the first year of the experiment, and since then only minor fluctuations have been recorded. In the grazed plot the percentages of bare ground and litter have shown considerable fluctuations in response to seasonal conditions. In 1947, 15·3 per cent. was recorded and in 1958, 8·7 per cent., but it will be seen from the form of the graph (14·9 per cent. bare ground and litter was recorded in 1957) that no permanent improvement has taken place.

In 1947, 1957, and 1958, the nature of the cover on each of the plots was investigated. The results are set out in Figure 2. We identify four classes of catchment cover, arranged in order of decreasing effectiveness, as follows:

(1) Living vegetation intermingled with and underlaid by dead plant remains.
(2) Living plants underlain by bare ground.
(3) Litter.
(4) Bare ground.

Figure 2 shows that the percentage of class 1 cover has increased in the fenced plot and has decreased in the grazed plot.

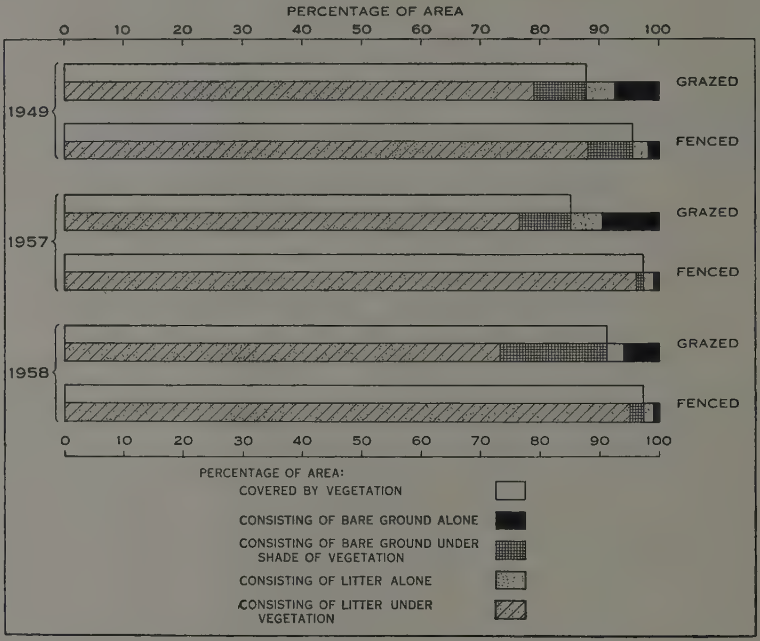

Fig. 2.—Grassland C—fenced plot and control. Point analysis: changes in the percentage of bare ground and in different types of cover over the period 1949–1958.

(*ii*) ***Luxuriance*** (Fig. 3)

Both plots have shown fluctuations in luxuriance in response to seasonal conditions. The initial slight difference in luxuriance shown by the plots has increased during the 11-year period of the experiment. Although the two plots show similar trends in luxuriance, the range of fluctuations is greater in the grazed plot. This feature is assumed to be a direct effect of grazing. It is to be noted that, although the luxuriance of *Poa* is largely independent of the grazing factor, the total luxuriance (all species) is depressed by grazing. The differences in luxuriance between the two plots in any year depend largely on the extent to which herbs develop, and this varies with the extent and pattern of the grazing. In good seasons, *Poa* flowers freely, and as cattle find the inflorescences palatable the herbs tend to be neglected. In unfavourable seasons the herbs make less growth than normal and, in addition, are heavily grazed.

It is to be expected that the grazed plot will continue to show big fluctuations in luxuriance. In the fenced plot, it is probable that fluctuations in luxuriance in response to purely seasonal conditions will become smaller with time, particularly if *Celmisia* continues to spread.

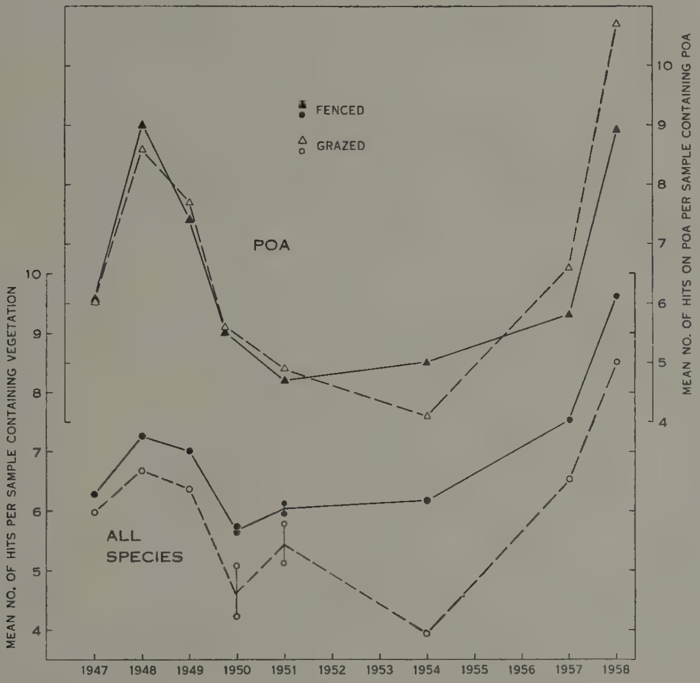

Fig. 3.—Grassland C—fenced plot and control. Point analysis: changes in *luxuriance* of the vegetation over the period 1947–1958.

(*iii*) *Percentage Overlapping Cover* (Figs. 4, 5)

The percentage overlapping cover provided by individual species in 1947 and 1958 is set out in Appendix I. Only the major species are discussed fully here.

A. POA (Fig. 4)

The percentage cover provided by *Poa* has fluctuated since 1947, but over the whole period of the experiment no definite trend in this has yet been identified in either of the plots. The data do not, of course, establish that *Poa* occupies exactly the same sites as at the beginning of the experiment, but from other observations we have made it is clear that *Poa* has, in fact, maintained itself on more or less the same ground as it occupied in 1947 and has colonized very little, if any, new ground in either of the plots. In short, *Poa* has not lost ground in the grazed plot, but, on the other hand, protection from grazing for 11 years has not produced the conditions necessary for the spread of *Poa* in the fenced plot.

In some years in both plots patches of *Poa* appeared to be dead, but most of these have been reoccupied by *Poa* plants which developed from small surviving shoots. Possibly there has been some seedling establishment, but its extent is unknown.

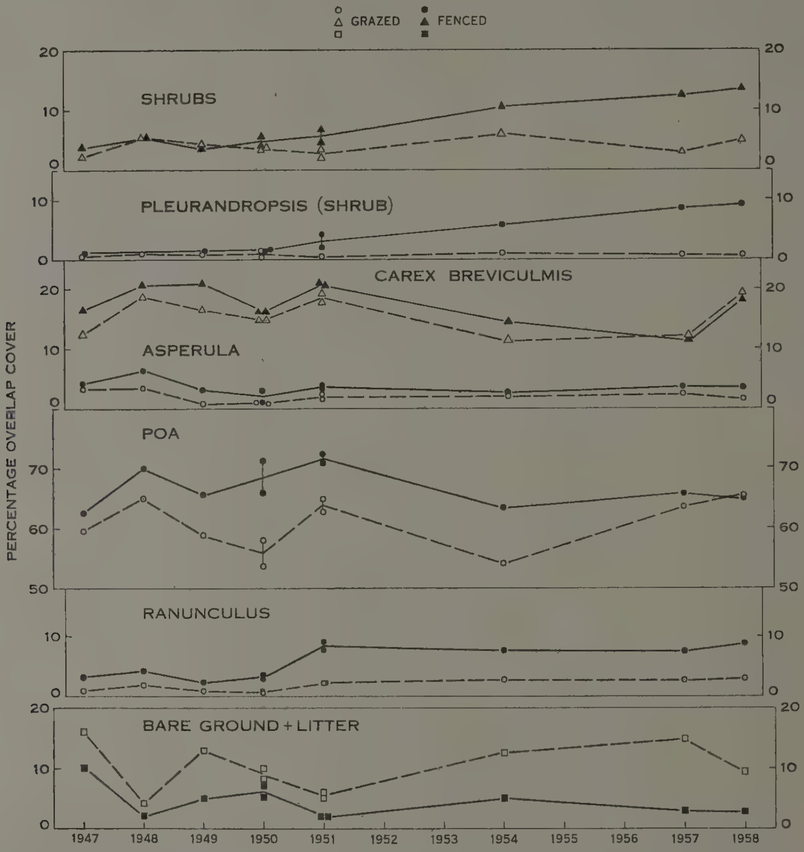

Fig. 4.—Grassland C—fenced plot and control. Point analysis: changes in the percentage overlap cover and in the percentage of bare ground plus litter over the period 1947–1958.

A very recent development in the fenced plot is that some small areas of degenerate *Poa* have been colonized by *Celmisia*. The graphs showing the cover provided by *Poa* between 1947 and 1954 are roughly parallel. This seems to indicate that the fluctuations recorded are mainly due to the effects of seasonal conditions on vegetative growth. In 1957 and 1958 the *Poa* of the fenced plot made a smaller response than the *Poa* of the grazed plot to favourable conditions. This effect appears to be due to the fact that in the fenced plot *Leptorrhynchus* and *Celmisia* are now competing strongly with *Poa*.

The convergence of the two graphs showing the cover provided by *Poa* is not significant in itself. However, when it is considered in conjunction with the graphs (Fig. 3) which show luxuriance of *Poa*, it can be taken as an indication that *Poa* is being adversely affected by prolonged protection from grazing. Between 1954 and 1958 the luxuriance figure for *Poa* in the grazed plot rose by 6·2, but over the same period the increase in the fenced plot was only 3·7. Since 1956, the *Poa* of the fenced plot has looked much less vigorous than that of the grazed plot and it appears likely, on the evidence available now, that *Poa* will show a sharp decline in the next few years in the fenced plot.

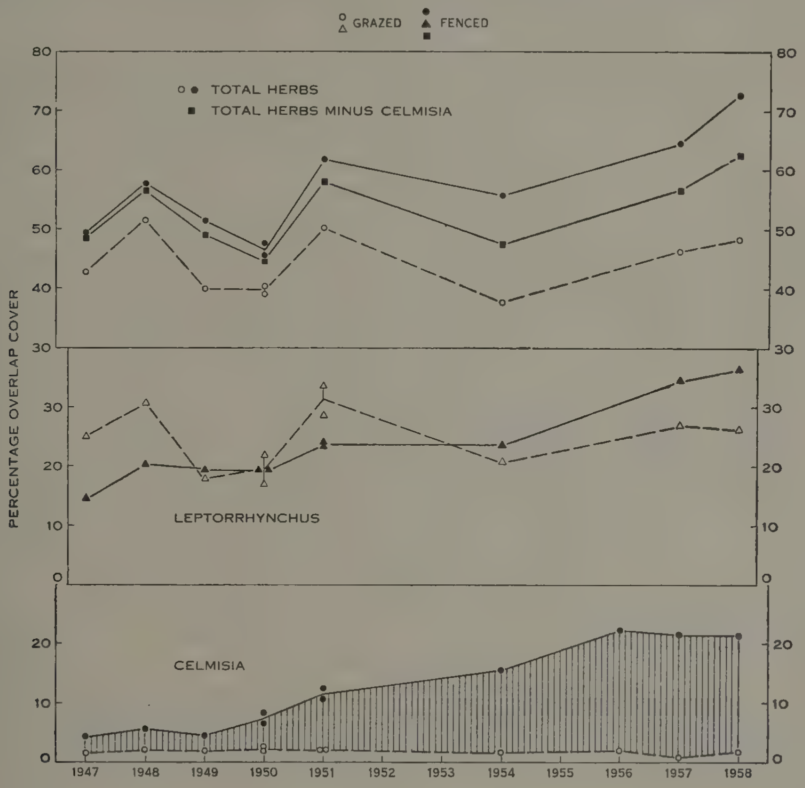

Fig. 5.—Grassland C—fenced plot and control. Point analysis: changes in the percentage overlap cover and in the percentage of bare ground plus litter over the period 1947–1958.

B. HERBS (Figs. 4, 5)

(1) General Remarks

Thirty-four species of herbs have been recorded for the plots. With the exception of one very minor species (*Stellaria multiflora*) all the herbs are perennial. All the important species and most of the minor species are common to both plots. Those which occur only on one or other of the two plots are at present unimportant species. They were present at the beginning of the experiment and have shown no changes which can be designated as significant. Collectively, the herbs are a conspicuous element in the vegetation, but most species individually contribute less than 2 per cent. of the cover. As this percentage is the same as our estimated maximum experimental error for all records obtained since 1951, it has not been possible to obtain accurate information about the amount of cover provided by all individual species throughout the experiment.*

In 1947, herbs contributed 49 per cent. of the overlapping cover in the fenced plot (i.e. herbs were recorded in 49 per cent. of the samples). Fluctuations have been recorded in response to seasonal conditions, but in only one year (1950) has the percentage of overlapping cover provided by herbs fallen below that recorded for 1947. There has been a marked tendency for the amount of cover provided by herbs to increase. In 1958, the cover provided by herbs was 73 per cent.

In 1947, in the unfenced plot 42 per cent. of the cover was provided by herbs. In 1958, herbs contributed 48 per cent. of the cover. In the intervening years percentages lower than the original one were recorded on three occasions. The graph (Fig. 5) shows that there has been no significant permanent change in the percentage cover provided by herbs during the period of the experiment.

The herbs which occur on the area have been considered as a group for the purpose of comparing their behaviour with that of *Poa* and of shrubs. Collectively, the herbs have been more important than any other type of plant in the re-vegetation of the fenced plot, but within the group individual species have shown considerable differences in behaviour.

In the grazed plot, the composition of the herb component of the vegetation has shown no significant change since the beginning of the experiment. The individual species are present in approximately the same proportions as in 1947.

In the fenced plot a considerable alteration in the composition of the herb component has been recorded since 1947. The changes are mostly due to the fact that *Leptorrhynchus* and *Celmisia* have made a big response to protection from grazing. The other herb species have shown little or no reaction.

(2) Behaviour of Individual Species

(i) *Leptorrhynchus squamatus* (Plate 1, Fig. 1; Plate 2, Fig. 2).—*Leptorrhynchus*, which is the most abundant herb on both plots, is a vigorous colonist of bare ground and of ground which supports only an open stand of other herbs. In the fenced plot the cover it provides has increased from 14 per cent. in 1947 to 36 per cent. in 1958 (Fig. 5). In the grazed plot it has fluctuated widely, but appears to have neither gained nor lost ground. The graph showing the cover provided by *Leptorrhynchus* in the grazed plot is almost parallel with that for the cover provided by all herbs in the same area. This can be taken as an indication that most of the herb species present have requirements similar to those of *Leptorrhynchus* and react as that species does to grazing and seasonal conditions. For the fenced plot the two comparable graphs are not parallel throughout. However, if for the fenced plot all the "herb" samples in which *Celmisia* is the only herb present are disregarded and figures are obtained for the percentage cover provided by "all herbs except *Celmisia*", the graph which can be plotted has the same general form as those which show the percentage cover provided by all herbs and by *Leptorrhynchus* in the grazed plot. From this it is clear that the "all herbs except *Celmisia*" component of the vegetation of the area shows a strong general response to seasonal conditions which is independent of grazing. If we now consider the graph which shows the percentage cover provided by *Leptorrhynchus* it appears that, in the absence of grazing, *Leptorrhynchus* is an aggressive species and can extend into territory occupied by other herbs.

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* The actual error involved is probably much less than 2 per cent. The consistency of the records for *Celmisia* in the unfenced plot and for shrubs in the fenced plot is supported by direct observations made on these plants.

In both plots the percentage cover provided by herbs rose in response to good seasonal conditions in 1948. In both cases the development of *Leptorrhynchus* paralleled that of the whole herb component. In 1949, which was a poor year for growth, the percentage cover due to herbs fell in both places. The fall was sharper in the grazed plot. We attribute this to heavy grazing of the herbs. In 1950, conditions for growth were again unfavourable; the percentage cover provided by herbs showed a further decline in the fenced plot, but in the grazed plot was not significantly different from the year before. It appears that heavy grazing in both seasons restricted the herbs almost to their minimum vegetative development. In the fenced plot, *Leptorrhynchus* did not lose ground in the two unfavourable seasons, although the total cover provided by herbs was less in 1950 than it was in 1947. Again, between 1951 and 1954 the percentage cover provided by *Leptorrhynchus* remained steady while the total cover provided by herbs decreased.

It is concluded that grazing prevents the spread of *Leptorrhynchus*, and that it is not as severely affected by adverse seasonal conditions as are many of the other herb species.

The luxuriance figures for *Leptorrhynchus* were 3·0 in the fenced plot and 2·9 in the grazed plot in 1947. During the period of the experiment the luxuriance of *Leptorrhynchus* in the grazed plot has been less than 2·9 in all except two years. In three seasons it fell as low as 2·3. In the fenced plot the luxuriance figure for *Leptorrhynchus* reached 4·5 in 1958 and, except in three of the early years of the experiment, has been consistently higher than the original reading.

(ii) *Celmisia longifolia* (Fig. 5; Plate 2, Fig. 2).—Although *Celmisia*, like *Leptorrhynchus*, has made a big advance in the fenced plot, it is not here a colonist of bare ground. In 1947, most of the *Celmisia* plants which were present on the plots grew closely surrounded by *Poa* tussocks and were quite small. This is still the case on the grazed plot, to which *Celmisia* contributed 1·5 per cent. of the cover in 1947 and 1·9 per cent. in 1958. The percentage cover due to this species did not alter during the course of the experiment.

In the fenced plot *Celmisia* increased its contribution to the cover from 4·4 per cent. in 1947 to 22·3 per cent. in 1956 (Plate 3, Figs. 1, 2). Since then it has made no further progress. It appears to be even less affected by adverse seasons than is *Leptorrhynchus*. Between 1951 and 1954 when *Leptorrhynchus* made no progress, *Celmisia* increased from 11 to 15 per cent. cover. On the other hand, it seems to be able to exploit favourable seasonal conditions only if the specialized sites it requires for colonization are available. *Celmisia* has increased its contribution to the cover in several ways. Plants which were present in 1947 have become larger and denser and have developed into large clumps. From these clumps rhizomes have spread into areas occupied by degenerate *Poa* and into others on which shrubs grew up after the plot was fenced. Invasion of areas occupied by shrubs and *Poa* was not observed in the early stages of the experiment, but it is becoming increasingly evident. Until now, *Celmisia* has made its major advance by occupying sites which were pioneered by *Leptorrhynchus* and other herbs, and on which they persisted for some years, presumably until they reached the degenerate phase of their life cycles. It is probable that the apparent failure of *Leptorrhynchus* to progress between 1951 and 1954, during which time the cover due to *Celmisia* increased, was due to active invasion of the oldest patches of *Leptorrhynchus* by *Celmisia*. In these patches *Celmisia* is now dominant and *Leptorrhynchus* has been almost completely suppressed.

The cover provided by *Celmisia* increased between 1954 and 1956, but since then the species has made no progress. Its failure to make headway in 1957 and 1958 probably reflects the limited development of *Leptorrhynchus* between 1951 and 1954. It appears likely that the rapid development which *Leptorrhynchus* has made since 1954 will have as its consequence a sharp rise in the percentage cover due to *Celmisia* in the next few years. The form of the graph for *Leptorrhynchus* suggests that this species is still increasing in the fenced plot. Direct observations indicate that *Leptorrhynchus* will not persist indefinitely on any one patch of ground in the absence of grazing, but that it is eventually invaded and suppressed by *Celmisia*. It appears likely, then, that the contribution made by *Celmisia* to the cover of the fenced plot will continue to increase for many years to come, and that it will become one of the dominant species of the area.

Once *Celmisia* is established it tends to suppress the other plants in its immediate vicinity. The young *Celmisia* plant is at first small and its leaves are almost vertical. As the rosette enlarges the older leaves ultimately assume a more or less horizontal position and the surrounding plants are either pushed aside or bent down to the ground. *Leptorrhynchus* and other herbs are readily suppressed in this way, and as a result *Celmisia* exhibits a strong tendency to occur unmixed with other herbs. This is clear if the graphs which show the total cover provided by all herbs including *Celmisia* and the cover provided by *Celmisia* (Fig. 5) alone are compared. The figures which were used to construct the latter graph were obtained by disregarding all the samples in which other herbs occurred.

The patches of *Celmisia* have not been established on the plot for a long enough period for the degenerate phase of the life cycle to develop, so we cannot be absolutely certain that some other species, at present inconspicuous or absent, will not replace *Celmisia* as *Celmisia* replaces *Leptorrhynchus*. In 1958, seedlings and young plants of *Ranunculus lappaceus* were numerous among the older *Celmisia* plants of the plot, but we do not think it is likely that *Ranunculus lappaceus* will become one of the dominant species of the community. It appears to us that the species which will probably exploit the degenerate and gap phases of *Celmisia* is *Poa australis*.

(iii) Other Species.—Only a few of the other herbs of the area are worthy of special mention.

Carex breviculmis (Fig. 4) is the most abundant of the minor herbs. It grows in between the tussocks in patches of *Poa* and also occurs alone in apparently sod-bound patches surrounded by bare ground. It has taken no active part in the colonization of bare ground in the fenced plot. In the grazed plot it is grazed closely where it forms patches, but is protected where it occurs with *Poa*. In the fenced plot it contributed 17 per cent. of the cover in 1947 and approximately 20 per cent. in 1948, 1949, and 1951. Although, on the whole, it has not shown violent fluctuations in response to seasonal conditions, the amount of cover provided by it has declined slowly until in 1957 it was responsible for only 11 per cent. The percentage rose sharply to 18 in 1958. The patches of this species which were present at the beginning of the experiment have been overgrown by *Leptorrhynchus*.

In the grazed plot, *Carex* contributed 12 per cent. of the cover in both 1947 and 1957. In the interim the fluctuations have paralleled those of the species in the fenced plot, and the parallel was again recorded in 1958, when 19 per cent. cover was recorded for the species. We conclude that *Carex breviculmis* has shown no recognizable trend in either plot.

Asperula (Fig. 4) is noteworthy in that it has shown little response to protection, for all that in certain circumstances it is grazed heavily. On the grazed plot *Asperula* has, in general, been protected by the *Poa* amongst which it grows and it has not been grazed to any great extent. It is grazed heavily only where it grows unmixed with living *Poa*. On the fenced plot it has been kept in check by competition from other herbs and from *Poa*. In grassland communities *Asperula* only grows thickly in mats of dead *Poa* which remain undisturbed. Where there are no large areas of dead *Poa* it straggles among the tussocks and is inconspicuous. It is readily suppressed by taller-growing plants. On both plots there have been patches of dead *Poa*, but they have been neither extensive nor persistent. *Asperula* has appeared on most of them, but as the patches have been recolonized by *Poa* or invaded by *Leptorrhynchus* or *Celmisia*, *Asperula* has been shaded out.

Senecio lautus is a species which has shown a decline in the fenced plot. In 1947, it contributed 6 per cent., and now accounts for only 1 or 2 per cent. of the cover. Like *Asperula*, it reaches its best development in grossly damaged swards of *Poa*. Otherwise it survives as small plants which grow out from the bases of tussocks. On the fenced plot its decline can be attributed to competition from more vigorous herbs. In the grazed plot it contributed 3 per cent. of the cover in 1947. Its contribution has undergone small fluctuations since, but has shown no significant change.

Ranunculus lappaceus (Fig. 4) was very inconspicuous on both plots in 1947. In the unfenced plot the cover it provides has increased from 1 per cent. in 1947 to 2·9 per cent. in 1958. In the fenced plot the cover has increased in the same time from 3 per cent. to 8·8 per cent. This increase has been comparatively steady. As *Ranunculus* is a small herb which has become more plentiful under conditions involving severe competition, the increase, though small, is possibly important. However, it is too early yet to estimate the ultimate importance of *Ranunculus* in the sward, and the slight increase recorded for the species in the grazed plot suggests that the increased amount of *Ranunculus* in the fenced plot may be due more to the effects of seasonal conditions than to protection from grazing animals.

C. SHRUBS (Fig. 4)

In the early years of the experiment shrubs were very inconspicuous in both plots. Although many of the plants appeared to be quite old, most of them were small, prostrate, and unthrifty. Shrub seedlings were very few. At the beginning of the experiment approximately 2 per cent. of the overlapping cover in the unfenced plot was provided by shrubs. Nine species were recorded and all have persisted. In 1956 shrubs contributed 4 per cent. of the cover. The graph shows that very small fluctuations have been recorded during the period of the experiment, and that the shrub component has not changed significantly. The two commonest species are *Grevillea alpina* and *Hovea longifolia*. *Pleurandropsis trymalioides* is present, but throughout the experiment it has not been recorded as contributing more than 1·1 per cent. of the cover in any year (Fig. 4).

TABLE 1

PERCENTAGE OVERLAPPING COVER PROVIDED BY SHRUBS

Species	1947	1948	1949	1950	1951	1954	1957	1958
Fenced Plot								
Kunzea	1·6	3·3	1·0	1·8	1·2	2·4	2·5	3·4
Pleurandropsis	0·8	—	1·2	1·4	1·9	5·9	8·6	9·2
Other shrubs	1·4	1·8	1·3	1·5	1·2	2·1	1·4	1·8
Total	3·8	5·1	3·5	4·7	4·3	10·4	12·5	14·4
Unfenced Plot								
All shrubs	2·2	5·4	4·1	3·6	4·2	6·0	4·0	4·6
Pleurandropsis	0·5	1·0	0·8	0·2	0·9	1·1	0·5	0·5

In the fenced plot shrubs provided 4 per cent. of the overlapping cover in 1947. Until 1951 they showed no reaction to fencing except that the plants looked healthier than their counterparts in the grazed plot. By 1954 the cover provided by shrubs had risen to 10·4 and by 1958 to 14·4 per cent. Table 1 shows that this increase is entirely due to *Pleurandropsis*. The rise shown by *Kunzea* in the first year (1·6 to 3·3) was not maintained. The sampling error for this plant is high, as it only occurs in dense patches along the northern boundary of the plot.

In 1946, *Pleurandropsis* was present as scattered established plants and as seedlings. The old plants were small and prostrate and, except where shoots were protected as they grew out from beneath grass tussocks, they were in a badly damaged state and were very unthrifty. We thought this was due to wind damage. However, it is now certain that trampling by stock is the main factor preventing the development of *Pleurandropsis* in grazed areas. The plant has somewhat fleshy leaves which are easily bruised and broken, and the cortex of the stem is soft. As the plants are slow-growing, damaged parts are not quickly replaced. Seedlings are never numerous, and as they occur only on bare ground they are not cushioned by other plants against trampling. Seedling mortality in grazed areas is very high.

The *Pleurandropsis* plants of the fenced plot reached a height of 6–7 in. by 1956. They were then small, dense, flat-topped shrubs, slightly taller than the surrounding vegetation. In general, their lateral spread appeared to be restricted by the herbs and grasses which grew close around them. Since 1956, *Pleurandropsis* and the other shrubs of the area have grown very little in height, and the formerly closed canopies of many of them have become open. It is possibly more accurate to say that they have been opened up, because the major gaps in their canopies have been made and are being enlarged by *Celmisia* rosettes. The rosettes are produced at the ends of rhizomes developed by the older *Celmisia* plants. These commonly occur at the margins of areas occupied by shrubs. We have found *Pleurandropsis*, *Lissanthe montana*, and *Kunzea muelleri* invaded by *Celmisia* in this way, and have no doubt that *Celmisia* will suppress the shrubs.

We have not investigated the reason for the invasion of shrubs by *Celmisia*. At first sight an explanation in terms of cyclic development (Watt 1947) seems reasonable. Once the shrub passes the phase of maturity and its vigour declines, the foliage thins out to the extent that sufficient light reaches the ground beneath to allow other plants, in this case *Celmisia*, to develop. This explanation is open to a number of objections. In other communities on the High Plains, shrubs in the degenerate phase of their life history assume the "ring" form because the central branches die and leave a gap in the centre of the shrub. Such a gap has not been seen to develop in shrubs less than 18 years old, and, in fact, many shrubs known to be older than this show no sign of it. The gap, once formed, is colonized by other species, usually grasses, which extend to form a circular patch. Unless the shrub is a species which produces roots from its shoots it eventually dies and is replaced by the species which colonized the gap.

In the fenced plot, one plant of *Olearia floribunda* which was large and well grown in 1947 has since assumed the ring form and snow grass has colonized the central gap. It differs in this from all the other shrubs of the plot. Invasion usually takes place *before* there is an obvious gap in the branch system, and *Celmisia* rosettes are to be found in shrubs in which the central branches are still vigorous. It is quite unusual to find that the centre of a shrub is the first part to be colonized by *Celmisia*. In view of these facts and the comparative youth of the shrubs which are being invaded, it is possible that the important factor determining the process is not the stage of development reached by the aerial parts of the shrubs, but the availability and aggressiveness of *Celmisia*. In the early years of the experiment the *Celmisia* plants which were present on the plot were neither numerous nor vigorous enough to colonize rapidly all the sites which were suitable for their growth.

The low stature of the shrubs, even after 11 years of protection, seems to indicate that the environment is not favourable to them, and it is precisely their small stature which makes them vulnerable to invasion and suppression by *Celmisia*.

Taller shrubs can maintain their local dominance until the degenerate phase of the life cycle, because their foliage is too far above the ground for *Celmisia* or other plants of similar habit to be able to make gaps in it.

Kunzea and *Hovea longifolia* are the only shrub species of the area which can be expected to escape complete suppression by *Celmisia*. In both species roots are produced from prostrate branches, and the death of the older portions of the plants does not, therefore, entail the death of the whole plant.

The failure of the other shrub species to make any progress in the fenced plot is due to a variety of causes. All except two or three of the established plants which were present in 1947 were small. They have been suppressed, but not killed, by competition from herbs and grasses which showed a more rapid response to fencing. The suppressed shrubs have flowered and fruited very poorly, not at all in some cases. No seedlings of any species other than those of *Pleurandropsis* were present in 1947. Since then no patches of bare ground of sufficient size to allow establishment of seedlings have occurred.

(*iv*) *Composition of the Sward*

A. POA AND HERBS

The graphs which show the changes we have recorded in the composition of the sward are set out in Figure 6. The contribution which any species or group of species makes to the sward is influenced by its relative abundance and by the density of its shoots (indicated by "luxuriance"). For this reason the contribution which a species makes to the sward should be considered in relation to the amount of overlapping cover it provides. For instance, the percentage cover provided by *Poa* has not altered a great deal in either of the plots during the course of the experiment, but its percentage contribution to the sward has shown considerable fluctuation. This is partly due to variations in the luxuriance of *Poa* (Fig. 3) but also depends on the extent to which other species developed in any particular season. In the years in which the herb component increased the contribution made by *Poa* decreased, and vice versa.

In the fenced plot the relative contributions made by *Poa* and herbs remained fairly steady until 1950. In the grazed plot over the same period, the composition of the sward varied considerably. In 1951 the percentage contributed by *Poa* declined sharply in both plots. In the fenced plot it remained steady until 1957, but rose slightly in 1958. This rise was chiefly due to an increase in the luxuriance of *Poa*. It was not associated with an increase in percentage cover. We consider that the change in the percentage of *Poa* in the sward (from 68 per cent. in 1947 to 58 per cent. in 1957) is a significant one.

In the grazed plot, after reaching its lowest point in 1951, the amount of *Poa* in the sward rose steadily to 80 per cent. (1958). The form of the graph suggests that no permanent change has occurred. Under present conditions it appears that *Poa* may contribute as little as 62 per cent. and as much as 81 per cent. to the sward, depending on the season.

Leptorrhynchus shows interesting differences in behaviour in the two plots. In the grazed plot its contribution to the sward has shown considerable variation and almost exactly parallels that of the whole herb component. In the fenced plot, it remained steady from 1947 to 1950, showed a sharp rise in 1951, and has since regularly contributed about 16 per cent. to the sward, despite the encroachment of *Celmisia* on the areas it has occupied longest.

The contribution made by *Celmisia* to the sward of the fenced plot increased steadily until 1954. Although its contribution to the sward for 1957 was the same as that for 1956, a decrease was recorded for 1958. This can be readily accounted for, because in that year seasonal conditions were unfavourable for the full development of *Celmisia*. It flowered very poorly, not only on the plots but throughout the whole of the High Plains. The general conditions were extremely favourable for the majority of the species of the area, and we had no difficulty in collecting viable seed from a great number of them. It is rather unusual to be able to do so. However, the heads of *Celmisia* we examined contained no viable seed.

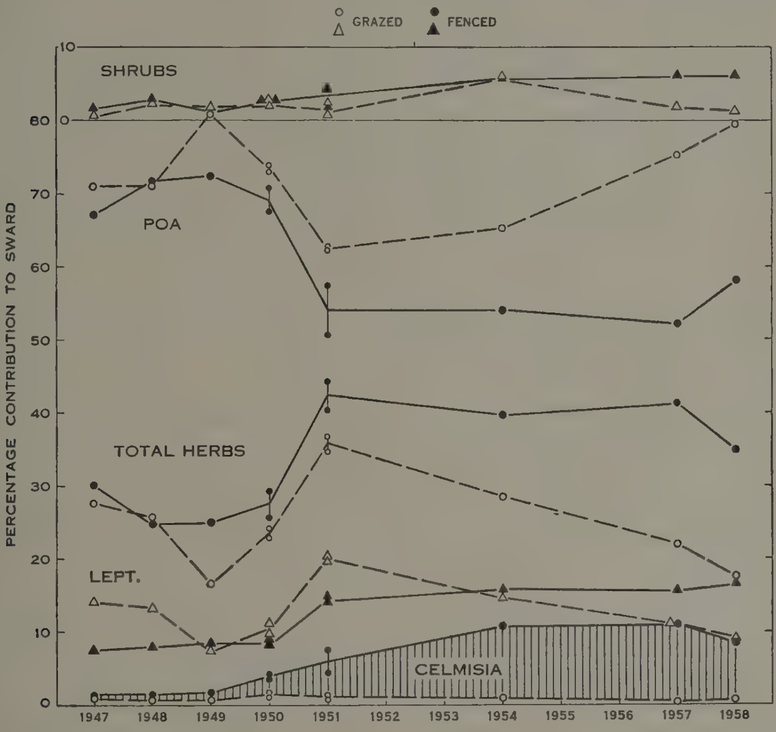

Fig. 6.—Grassland C—fenced plot and control. Point analysis: changes in the percentage contribution to the sward over the period 1947–1958.

B. SHRUBS

Shrubs make smaller responses than either grasses or herbs to seasonal conditions. In a favourable season their response may be masked by the far greater development of the other plants. In an unfavourable season the contribution shrubs make to the sward rises because the herbs and grass fail to reach their maximum

TABLE 2
GRASSLAND C SOILS, FEBRUARY 1957

Grazed Area						Fenced Area					
Sample No.	(1) Field Water Content	(2) Wilting Point	(3) Water Available in Field	(4) Sticky Point*	(5) Organic Matter	Sample No.	(6) Field Water Content	(7) Wilting Point	(8) Water Available in Field	(9) Sticky Point*	(10) Organic Matter
	(water per 100 g soil)				(%)		(water per 100 g soil)				(%)
1	24·67	18·92	5·75	29·3	8·91	1	27·50	17·66	9·84	26·2	6·59
2	23·30	17·04	6·26	33·8	8·92	2	28·50	22·15	6·35	27·4	7·65
3	24·96	18·10	6·86	32·0	8·99	3	30·36	23·33	7·03	40·2	12·67
4	23·03	17·04	5·99	31·5	8·80	4	29·95	20·08	9·87	39·8	11·52
5	21·11	22·29	−1·18	28·7	8·31	5	25·00	22·15	2·85	39·1	10·49
6	24·14	17·03	7·11	31·0	8·45	6	26·86	24·96	1·90	40·6	12·22
7	18·92	15·68	3·24	33·1	8·75	7	25·23	26·09	−0·86	40·2	12·28
8	25·63	18·25	7·38	31·6	8·73	8	27·53	23·69	3·84	—	12·82
9	24·74	18·23	6·51	33·8	9·25	9	27·04	22·43	4·61	44·5	14·58
10	24·76	18·84	5·92	33·9	9·45	10	25·67	21·12	4·55	39·9	11·95
11	19·39	25·06	−5·67	25·5	8·94	11	37·50	28·89	8·61	43·9	13·10
Mean	23·15	18·77	4·38	31·3	8·86	Mean	28·29	22·96	5·33	38·2	11·44

Samples:	1, 7, 11	Samples:	6, 7, 8
Colour:	Dry 5 YR 4/4 Reddish Brown Wet 5 YR 2/2 Dark Reddish Brown	Colour:	Dry 7·5 YR 3/2 Dark Brown Wet 10 YR 2/2 Very Dark Brown
Texture:	Clayey sandy loam	Texture:	Sandy loam

Statistical comparisons (*t*-test): columns 1, 6—$P<0\cdot001$; columns 2, 7—$P<0\cdot01$; columns 4, 9—$P<0\cdot01$; columns 5, 10—$P<0\cdot01$.

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* For these soils, water content at the sticky point is probably much lower than that at field capacity; this may reach 57 per cent. of the oven-dry weight (Table 4).

development. This is the explanation of the fluctuations shown by the shrub component in the grazed plot since 1950. In the fenced plot, despite the factors mentioned above, the shrub component has increased slowly in importance since 1950. Although the total luxuriance for the fenced plot rose sharply in 1958, the contribution made by shrubs to the sward did not decline. It is now 6·2 per cent.

(*v*) *Soils*

Field observations made in 1947 showed that the soil of both plots and of the surrounding area was a fairly uniform reddish brown clayey, sandy loam. Organic matter decreased and clay increased with depth, but there was no marked differentiation in the profile. It closely resembled soil from other areas of grassland C. In 1957, after a long dry spell (57 days with only light falls of rain), it was apparent that the soil of the fenced plot was appreciably wetter than that of the grazed area around it. Soil samples were, therefore, taken from each plot (see Section II) and the results of analysis are set out in Tables 2 and 3.

In 1958, as a check, further samples were taken from the contiguous boundaries of both plots (see Section II) and the results are given in Table 4.

The recorded differences in soil characters are due mainly to the greater accumulation of organic matter in the fenced plot and its incorporation in the soil. The rapidity with which this has occurred is surprising, in view of the severe conditions which prevail in the area, and must be taken as indicating the presence of an extremely active soil fauna and microflora. The differences in colour and texture shown by the soils of the two plots are so marked that the origin of 20 of the 22 samples could be decided on appearance alone. The two samples for which this could not be done were Nos. 1 and 2 from the fenced plot. They were obtained from the eastern end, a part of the plot which showed very severe erosion at the time of fencing and on which the vegetation has become luxuriant only in the last few years.

The differences recorded in field moisture content (Table 2) reflect differences in the wilting points of the soils rather than in the amounts of water available to plants at the time of sampling. As the samples were obtained at the end of an almost rainless period of 57 days, it is not surprising that many of them were near the wilting point and some were below it.

For 1957, the differences between the means for bulk density of the soils from the grazed plot and the fenced plot are highly significant. They remain so even when the samples obtained from bare ground are not taken into consideration. The high bulk densities of the samples from bare ground can be attributed to loss of topsoil with exposure of the denser layers beneath, and also to compaction by trampling. However, even where dense vegetation is present on the grazed plot, the bulk density is higher than in the fenced plot. This is probably due as much to compaction by trampling as to loss of organic matter.

In 1958, the differences between the two plots (Table 4) were again highly significant for bulk density and also for field capacity. These results from samples taken in such a pattern provide evidence to show that the marked differences between the soils of the fenced and grazed plots are associated with the fencing and not with any initial gradient of soil properties across the experimental area.

(*b*) *General Conclusions*

(i) *In the grazed plot*, great variations in the composition of the sward have been recorded throughout the experiment. There has been a consistent increase in the percentage of *Poa* and a decline in the importance of the herb component. It is too early to say whether this is a real trend or is due solely to the effects of seasonal conditions.

TABLE 3

BULK DENSITY OF SOILS, GRASSLAND C, 1957

Type of Cover	Bulk Densities	
	Grazed Plot	Fenced Plot
Poa	0·60, 0·87, 0·65, 0·41, 0·66, 0·61, 0·65	0·72, 0·52, 0·48
Poa and *Leptorrhynchus*	0·67, 0·63	
Leptorrhynchus	0·81, 0·82, 0·65, 1·02, 0·93, 0·86	0·72, 0·36, 0·48
Gnaphalium	0·63	
Kunzea	0·79, 0·71	
Grevillea	0·95, 0·87, 0·66	
Pleurandropsis	—	0·52, 0·54, 0·45
Celmisia	—	0·50, 0·42, 0·61
Bare ground	0·95, 0·91, 1·04, 1·00, 0·96, 0·83	
Mean	0·78	0·53

Statistical comparisons:

(1) (*t*-test)

(*a*) All samples $P < 0 \cdot 001$

(*b*) All samples except those including bare ground $P < 0 \cdot 001$

(2) Maximum deviation at 5% level, $\pm L = 0 \cdot 10$

Since 1945, when the experiment was begun, some official control has been exercised over the numbers of cattle allowed to enter the area, and the length of the grazing season has been curtailed. Many of the graziers have taken advantage of a sequence of good seasons to keep their cattle in their home paddocks, and have not sent them to the High Plains for the summer. These factors have operated to reduce grazing intensity within the area. Those of our records which are concerned only with the behaviour of plant species and the amounts of completely bare ground indicate that the present light rate of stocking is effective in more or less maintaining the *status quo*, but a rather alarming feature is the slow decline (from 78 to 72 per cent.) since 1949 in the amount of class 1 cover in the grazed plot (Fig. 2).

(ii) *The vegetation and soils of the fenced plot* have shown rapid changes in response to protection from stock. The changes recorded to date are beneficial, as they have resulted in the development of an almost complete cover of dense vegetation.

TABLE 4

BULK DENSITY AND FIELD CAPACITY OF SOILS, GRASSLAND C, 1958

Grazed Plot			Fenced Plot		
Sample No.	(1) Bulk Density	(2) Field Capacity (water/100 g soil)	Sample No.	(3) Bulk Density	(4) Field Capacity (water/100 g soil)
1	0·88	46·9	1	0·76	54·9
2	0·95	38·0	2	0·74	46·9
3	0·89	48·9	3	0·70	46·3
4	0·99	38·2	4	0·82	45·5
5	0·96	39·5	5	0·72	47·8
6	0·90	44·2	6	0·79	46·8
7	1·02	34·6	7	0·75	50·6
8	0·97	40·7	8	0·75	53·5
9	0·94	43·2	9	0·83	45·6
10	0·93	43·2	10	0·76	52·7
11	0·93	39·3	11	0·68	57·0
Mean	0·94	41·5	Mean	0·75	49·8

Statistical comparisons (*t*-test):
Columns 1, 3 $P < 0{\cdot}001$
Columns 2, 4 $P < 0{\cdot}001$

After an initial period (1947–1951) in which the vegetation of the fenced plot showed considerable variation in composition from year to year, a relatively steady state was reached. Since then only minor changes in the proportions of the major components have been recorded. The net effects are an increase in the herb and shrub components and a decline in the importance of *Poa* in the sward.

The most important reaction has been an increase in the amount of cover provided by herbs, especially by *Celmisia*. It is obvious that grazing is seriously limiting the development of herbs, which are the most effective plants of the community in the colonization of bare or thinly vegetated soil (Plate 3).

The results show that the vegetation of the fenced plot is much more stable than that of the grazed plot. The amounts of bare ground and of ground covered only by litter do not increase to any extent in poor seasons, nor does the total luxuriance decline sharply, as it does in the grazed area.

The stability of the vegetation of the fenced plot in poor seasons is at present mainly due to the fact that whatever growth the plants make is not grazed off, but it is also due in part to the fact that certain species, notably *Celmisia*, *Leptorrhynchus*, and *Pleurandropsis*, which have become well established in the fenced plot, are not seriously depressed in poor seasons. *Celmisia*, in particular, forms a very conservative element in the vegetation.

The alterations in the physical properties and water relationships of the soil after only 11 years of protection are striking. Presumably the improvement is connected with changes in the type of cover present. Lowdermilk (1929) showed that the presence of litter on the surface of a forest soil has the effect of maintaining the infiltration capacity of the profile at the maximum. In grassland C maximum infiltration is to be expected only where there is class 1 cover. In the fenced plot 93 per cent. of the area now carries class 1 cover, but for the unfenced plot the figure is 73 per cent. Moreover, the cover in the fenced plot is richer in *Celmisia.* Preliminary experiments suggest that snow grass, with its intricate mass of fine leaves, intercepts a higher proportion of the summer rainfall than does *Celmisia*, whose leaves tend to funnel water into the soil.

The improvement in cover has been accompanied in the soil by an increase in organic matter, an increase in field capacity, and a decrease in bulk density. If these changes could be induced over large areas the consequences in terms of the general hydrology of the catchment would probably be considerable.

IV. The Status of Grassland C, with Special Reference to Erosion

(a) *Erosion*

Grassland C is undoubtedly eroded, mainly by wind, and very different grades of surface erosion are found within a few yards of traverse (see Plates 1 and 2). Evidence for the existence of erosion is as follows:

(i) Throughout grassland C the grass tussocks and many of the herbs are rooted in soil which is 1–4 in. higher than the surface of adjacent bare ground (Fig. 1). The level of the soil under the grass is usually higher than that occupied by herbs.

(ii) The soil of the bare patches often contains dead roots which are not those of living plants growing nearby.

(iii) On the south-east margin of each patch of bare ground there is an accumulation of small stones and gravel which has been blown across the patch and has been prevented from travelling further by the vegetation (Fig. 1). The finer materials of the soil are blown away. Soil can be seen blowing on dry days, particularly in areas which have been recently disturbed by the passage of vehicles or by the trampling of travelling or grazing stock.

(iv) Some of the herb species are not natural in the community. In the United States* the appearance of xeric lowland species at elevations beyond their normal range is taken as an indication that serious disturbance of the vegetation has occurred.

We have tentatively divided the herbs of grassland C into three main groups, as follows:

A. Herbs which were originally present but inconspicuous. This group includes the colonists of bare ground or of mats of dead grass. Examples: *Leptorrhynchus*, *Asperula*, *Craspedia* spp., *Senecio*, *Ewartia*, *Claytonia australasica*.

B. Herbs which were originally abundant but which have become rare. Examples: *Podolepis* spp., *Aciphylla glacialis*.

C. Herbs from lower elevations, not present in the original sward. Examples: *Hypochoeris radicata*, *Rumex acetosella*, *Agropyron scabrum*, *Picris hieracioides*.

Picris hieracioides, *Hypochoeris radicata*, and *Rumex* are of European origin and they, with the native *Agropyron scabrum*, became very prominent on badly damaged areas at the margins of the High Plains after the 1939 fires. It is apparent that they can only maintain themselves in the area on severely disturbed ground. We have reasonably good evidence that *Leptorrhynchus* was not a prominent plant on the High Plains before 1900. It is said to have "thickened up" since then and we have ourselves observed that it is still extending its range on the High Plains. *Ewartia nubigena* is recorded (Ewart 1930) as a rare plant, but it is now common on eroded ground in many parts of the High Plains. Tadgell (1922) recorded *Rumex acetosella* as occurring between 5000 and 6000 ft on Mount Feathertop, but the species had apparently been present in the area for a considerable time as he writes of it: "On mountain tops the common sorrel is almost as plentiful in places as is St. John's Wort in the Ovens Valley lower down". He continues: "We were very much struck with the rapid increase of aliens among the alpine plants. At one time stray plants of sorrel, dock, thistles and even goosefoot, might be seen here and there, but now acres are taken up by docks, sorrel, flatweed, hogweed and other lowland stock-brought undesirables. . . . This increase has doubtless been caused by the larger number of sheep and cattle now sent to the alpine heights . . . during the summer season". *Rumex acetosella* has probably been present on the High Plains for many years, but it was nowhere abundant until after the 1939 fires. From then on until about 1947, it was so abundant in many parts of the area that whole hillsides and some mountain tops took on a red colour when it was in flower. It has since become much less conspicuous.

The occurrence and abundance of the plants mentioned above made it obvious that we were dealing with a community which had suffered gross disturbance, to the extent that plants which are recognized as colonizers of bare ground were able to enter it and in some places to assume dominance. Certain native herbs which are now rare or at least uncommon were formerly abundant. Skene and Smyth

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* Personal communication from the late Dr. L. Ellison, Chief, Intermountain Research Station, Utah.

(1874) recorded *Euphrasia scabra* R.Br. as one of the more conspicuous plants on Mt. Hotham; it is now extremely rare in the area. According to old cattlemen, *Podolepis robusta* was also a common species, but heavy stocking of the Plains during the 1900–1901 drought seriously reduced both it and *Aciphylla glacialis*. This latter species is extremely palatable to horses and to cattle. Since the exclusion of grazing on the upper slopes of Mt. Kosciusko (N.S.W.) it is increasing in abundance. It was reported on Mount Hotham by Skene and Smyth (1874) as "in many places but nowhere thickly until we reached the slopes". In 1922 Tadgell ascribed its rarity to the effects of grazing.

(*b*) *The Derivation of the Community*

Our original assumption was that grassland C was derived from grasslands A and B through degeneration of the sward. We considered it probable that the bare ground, and that at present occupied only by herbs, originally carried grass, because one of the earliest consequences of severe damage in grasslands A and B is an increase in the herb component of the sward (paper III of this series). This view was supported by information supplied by some of the older retired cattlemen to the effect that a "blue" grass which was common on the High Plains (in particular in Pretty Valley) in the early days of grazing had disappeared as the result of selective grazing. The only obvious "blue" grasses still existing are, however, *Trisetum spicatum* and the glaucous forms of *Poa australis*, none of which is heavily grazed.

We have recently learned that an early local name for *Celmisia* is "blue grass", and this, coupled with a traditional belief that Pretty Valley (grassland C) was always rich in herbs (hence its name), provides some support for our present view, that grassland C has been derived from a herb-field community, in which *Poa* and *Celmisia* were codominant. The major evidence for this comes from the results of the fencing experiment.

Plant communities rich in *Celmisia* were formerly present on top of Mount Hotham (Skene and Smyth 1874), and herb-fields in which *Poa* and *Celmisia* occur as codominants are still to be found on exposed slopes at higher elevations than Pretty Valley as, for instance, on Mount Nelse and Mount Bogong. Where the two species occur together they form a mosaic of separate patches. Small *Poa* plants can be found in old patches of *Celmisia* and *Celmisia* can be seen to invade weak patches of *Poa*. With increasing elevation *Celmisia* becomes more important than *Poa*. Small shrubs and other species of herbs are also present, but these areas are not so rich in species as are the more extensive herb-fields of Mount Kosciusko.

On Mount Nelse and elsewhere on the High Plains stock selectively graze *Celmisia* even where it is present in very small amounts. It is common to find that whole shoots are pulled out and discarded. Heavy concentrations of stock on the High Plains in drought years could account for the destruction of a great deal of the *Celmisia* originally present, but grazing and uprooting of plants in seasons in which *Poa* did not flower has undoubtedly contributed to the reduction of *Celmisia* to the status of an occasional species in most of the area occupied by grassland C. It is not yet clear why *Celmisia* has persisted on parts of Mounts Nelse and Bogong, yet has been so much reduced in Pretty Valley and Mount Hotham.

As a result of experiment and supporting observations the following is proposed as the history of grassland C.

The original vegetation consisted of *Poa*, *Celmisia*, and a group of herbs (group A). *Aciphylla glacialis* was probably abundant, but we have little information about other species which may have been present. The herbs of group A were eliminated by grazing and *Celmisia* was reduced. The progressive removal of *Celmisia* and other herbs exposed bare ground, which neither *Poa* nor *Celmisia* nor the herbs of group A were capable of colonizing. Another group of herbs (group B), of which *Leptorrhynchus* is the most important species, slowly colonized the bare ground, but their development has been seriously limited by continued grazing.

Under present day conditions the degeneration of the former herb-field is not as rapid as it was initially. The vegetation has reached some sort of equilibrium and has the following composition: *Poa c.* 70 per cent., herbs (group B) *c.* 20 per cent., *Celmisia* 1–2 per cent. The amount of bare ground varies locally and in response to seasonal conditions between 5 and 20 per cent.

If grazing stops, the community can be expected to show the following developments. The herbs of group B will rapidly colonize the bare ground and will persist until replaced by *Celmisia*. Group B will slowly diminish in importance, in the end remaining only as traces. Group A may or may not return, depending on the availability of seed.

Shrubs present a special problem. In both herb-field and grassland C, trees are absent and shrubs are usually sparse, stunted, and unthrifty. This contrasts with the position for the more scattered grasslands B and B_1, in which shrubs may grow tall and assume local dominance. We suppose that wind pruning is the major factor which militates against a development of woody plants in grassland C. Where shrubs occur around outcrops of rock they assume an espalier form on the windward side, but grow taller than the herbs and grass where they receive shelter. Under the severe conditions on eroded mountain tops many shrubs make effective growth only in the shelter of grass tussocks.

Although, as we have seen, shrubs have increased in importance in the fenced plot, we consider it likely that they will play only a minor part in the regeneration of the community, and will reach their greatest development in the early stages of the process. They are mostly established on areas of bare ground of a size that can be rapidly colonized by herbs, spreading vegetatively. Even when protected from stock the shrubs grow very slowly, remain wind-pruned, and have to compete with taller and more vigorous herbs. As bare ground is usually required for the establishment of shrub seedlings, their opportunities for regeneration are becoming more limited as the vegetation closes.

However, there are occasional patches of dense and fairly tall shrubs in some parts of grassland C, and we believe that these became established on areas where soil erosion was so severe that herbs were unable to spread fast enough to compete with seedling shrubs. Presumably, under such conditions some of the shrubs form a wind break and protect the others. The importance of shrubs in the regeneration of grassland C may well depend on the extent to which the original community was damaged. The greater the disturbance, the more important the shrubs are likely to be in the succession.

V. Catchment Management on the High Plains

Active management of this catchment to increase water yield, or for other purposes, must be left for the future, when it is hoped that sufficient information will be available for management to be undertaken on a scientific basis. The only aims possible at present are the improvement and conservation of the vegetative cover of the catchment. This involves the development of a complete and relatively stable cover of vegetation.

At present, in the greater part of the area occupied by grassland C, the nature of the damage to the sward is such that the patches of bare ground are small and separate. The chief agent of soil erosion is wind, which scoops the finer particles from the bare hollows. However, if grassland C is allowed to degenerate further, to the extent that the patches of bare ground enlarge and link up, removal of soil by running water will become increasingly important. This will greatly reduce the efficiency of the catchment, but perhaps more important still is the fact that as erosion proceeds repair of the damage will be increasingly difficult. Already, small areas of grassland C have been damaged to such an extent that shrubs are the only plants capable of recolonizing them. Shrubs are less desirable than herbs or grasses as catchment cover—they are slow-growing, provide sparse litter and humus, and burn readily. The burning of a shrub community bares the soil and makes the development of a sward still more difficult.

Grassland C is one of the most extensive communities of the High Plains area. The present rate of stocking with cattle is maintaining it in a state in which it gives less than the maximum possible protection to the soil, and under conditions in which no improvement is possible. We have, therefore, elsewhere recommended that grazing of this community be prohibited.

In most of the areas occupied by grassland C, complete vegetative cover and minimal soil loss could be developed by excluding cattle for approximately 10 years, but a much longer period of protection would be necessary for the development of a stable type of vegetation. In spite of the excellence of the cover now present on the fenced plot in Pretty Valley, a renewal of grazing would cause it to revert in a very few years to a state little different from that of the grazed plot.

VI. Acknowledgments

We have earlier recorded our great indebtedness to the Victorian State Electricity Commission and to the Victorian Soil Conservation Authority. In the extensive field work involved in the present study we have been greatly assisted by present and past students and members of the staff of the Botany and Agriculture Schools, University of Melbourne. It is impossible to mention everyone individually,

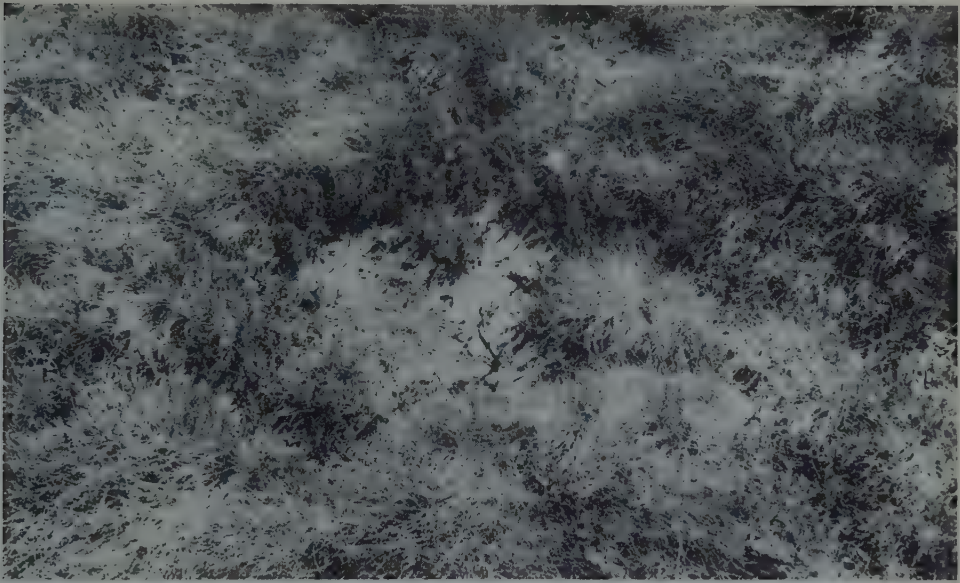

Fig. 1.—Grassland C. Stage 1 of erosion. Bare ground in centre and top middle, with caked soil surface disturbed by hoof mark. *Leptorrhynchus squamatus* growing out from the margins of snow grass tussocks.

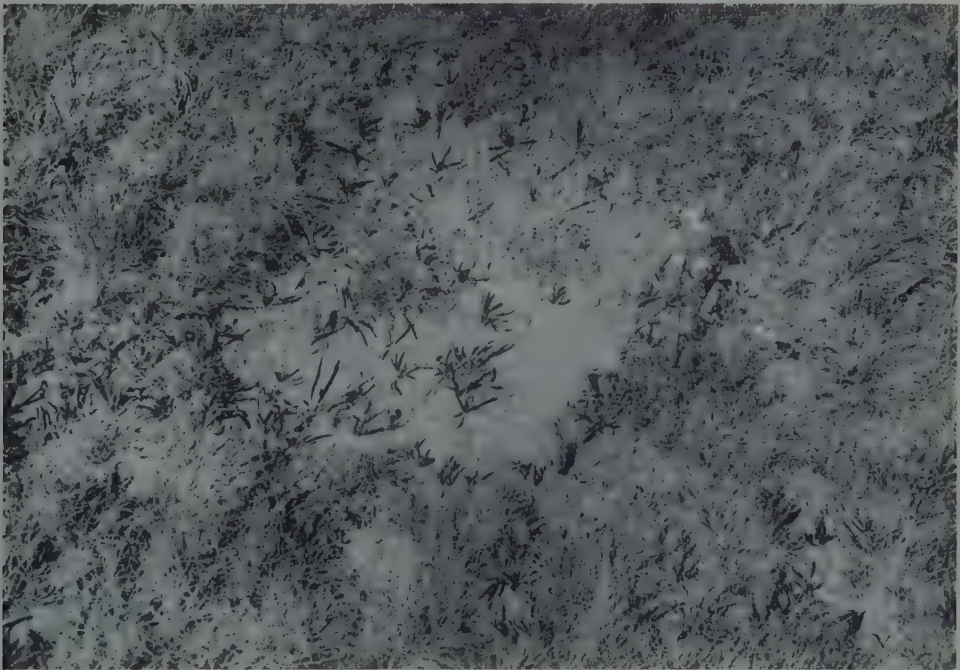

Fig. 2.—Grassland C. Stage 2 of erosion. Snow grass tussocks reduced in size, much bare ground, colonized in centre by seedlings of *Microseris scapigera*. Small prostrate plant of *Pleurandropsis trimalioides*, centre right.

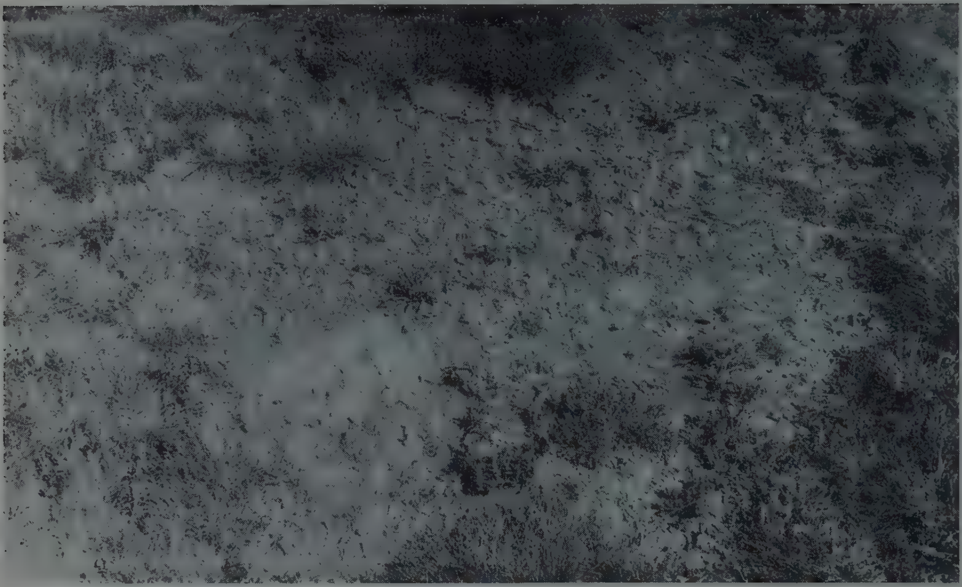

Fig. 1.—Grassland C. Stage 3 of erosion, showing the great reduction in cover provided by snow grass, large areas of bare ground with little colonization by herbs.

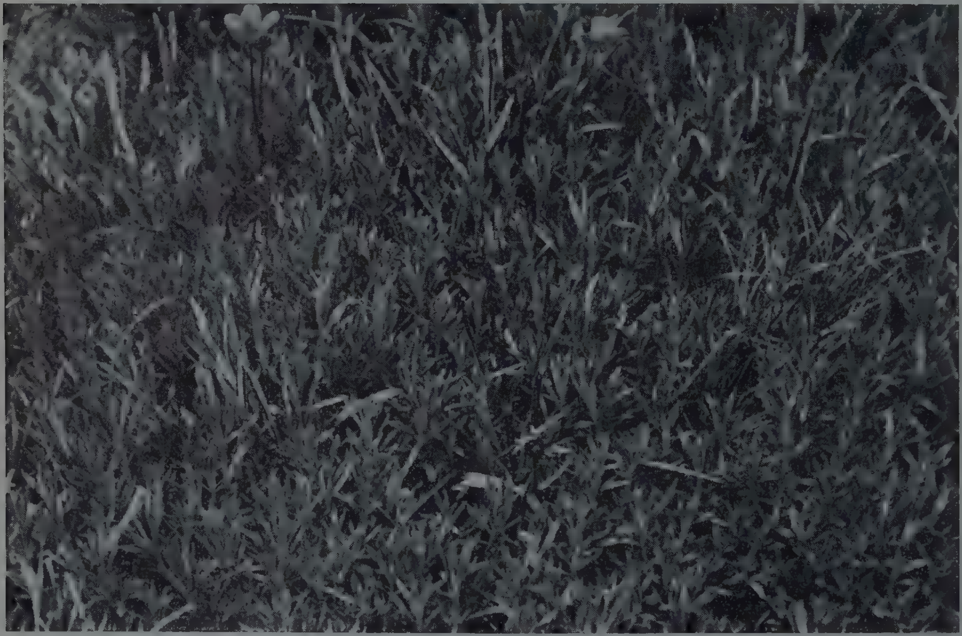

Fig. 2.—Grassland C. *Leptorrhynchus squamatus* dominant in 1957 on ground which was bare in 1947. *Ranunculus* is also present and *Celmisia* has begun to enter.

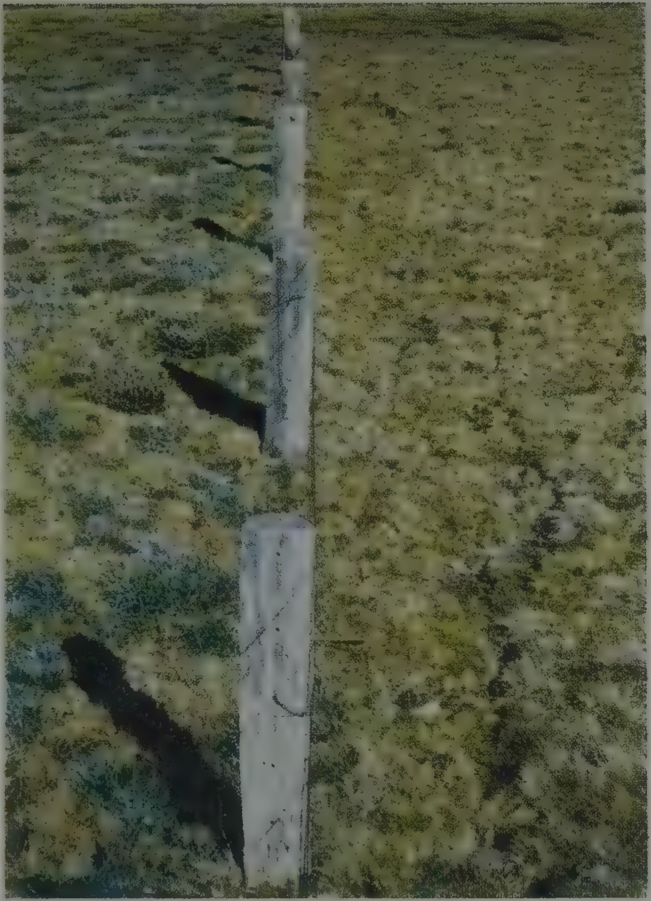

Fig. 1.—Grassland C, plot in 1957. Right of fence: grassland C, grazed. Left of fence: inside the plot, ungrazed for 10 years, showing development of closed vegetation, rich in *Celmisia* (bluish foliage).

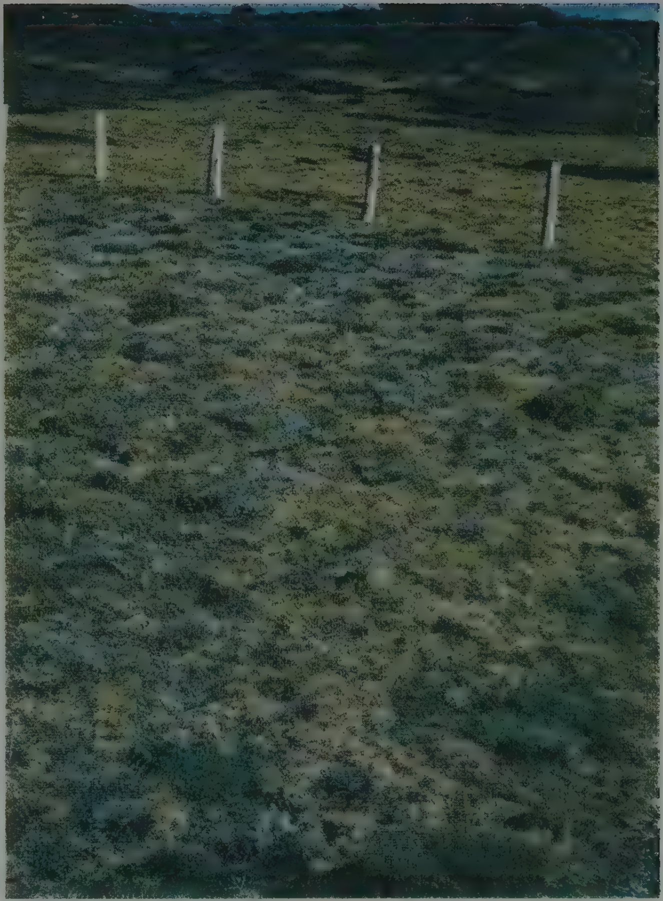

Fig. 2.—Grassland C. View across fenced plot in 1957, showing abundance of *Celmisia* and a foreshortened view of grazed grassland C outside the fence. Shrub communities on rise in background.

for the list includes more than 70 people, to all of whom we are grateful. We owe special thanks to Associate Professor G. W. Leeper and Mr. B. Cockcroft (who advised and assisted respectively on the soil work), to Dr. D. J. Carr (for assistance with the manuscript), and especially to the following for untiring field work: Mrs. H. H. Bennett, Mrs. C. E. Christianson, Mrs. H. Crowley, Mr. T. Derham, Mrs. S. C. Ducker, Dr. S. L. Duigan, Mrs. A. M. Kelso, Miss H. M. Purnell, Dr. M. J. Mayo, Dr. N. F. Millis, Dr. G. R. Raw, Dr. D. H. Ashton, Dr. H. T. Clifford, Mr. B. V. Fennessy, Dr. D. W. Goodall, Dr. K. S. Rowan, and Mr. S. Weatherhead.

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APPENDIX I

PRETTY VALLEY PLOTS (GRASSLAND C): PERCENTAGE OVERLAPPING COVER PROVIDED BY INDIVIDUAL SPECIES, 1947 AND 1958

+ Indicates that the species occurs
— Indicates that the species was not recorded

Species	Grazed Plot		Fenced Plot	
	1947	1958	1947	1958
(1) Monocotyledons				
(*a*) grasses				
Agrostis venusta Trin.	0·4	0·2	0·9	0·5
Agropyron velutinum Nees.	1·7	1·0	1·8	0·8
Danthonia nudiflora P. F. Morris	1·5	0·9	6·2	2·5
Poa australis sp. agg.	59·6	65·4	62·7	64·8
Trisetum spicatum (L.) Richt.	+	1·2	0·1	2·1
(*b*) other herbs				
Carex breviculmis R. Br.	12·3	19·3	16·6	18·1
C. hebes Nelmes	0·6	0·2	3·4	2·7
Hypolaena lateriflora Benth.	+	+	1·5	1·1
Luzula campestris DC.	+	0·5	0·5	+
Prasophyllum tadgellianum Rogers	+	+	+	+
(2) Dicotyledons				
(*a*) herbs				
Asperula gunnii Hk. f.	3·3	1·7	4·1	3·5
Brachycome decipiens Hk. f.	0·2	0·3	1·2	1·1
B. scapiformis DC. (*B. aculeata* (Lab.) Less.)	+	+	+	+
Cardamine (undescribed sp.)	+	+	+	0·2
Celmisia longifolia Cass.	1·5	1·9	4·4	21·4
Colobanthus apetalus Black	+	+	0·1	0·5
Cotula filicula Hk. f.	+	+	+	+
Craspedia uniflora Forst.	0·4	1·4	0·8	0·8
Erigeron pappochroma Lab.	0·2	0·3	0·5	0·8
Euphrasia antarctica Benth.	+	+	+	0·5
Gentianella diemensis (Griseb.) J. H. Willis	+	+	0·1	0·8
Geranium pilosum Forst. ex Willd.	+	+	0·2	+
Gnaphalium collinum Lab. var. *radicans* F. Muell. ex Benth.	+	+	0·9	1·9
Goodenia hederacea Sm.	1·0	1·2	+	+
Helichrysum bracteatum Andr.	+	+	+	+
Leptorrhynchus squamatus Less.	25·2	26·2	14·4	36·3
Microseris scapigera Sch.-Bip.	2·0	0·2	2·7	0·7
Oreomyrrhus andicola (H., B., & K.) Endl.	0·2	0·9	0·1	0·8
Podolepis robusta (Maid. & Betche) J. H. Willis	+	+	+	0·2
Poranthera microphylla Brongn.	0·4	+	0·3	0·7
Plantago tasmanica Hk. f.	0·6	0·7	0·7	1·6

APPENDIX I (*Continued*)

Species	Grazed Plot		Fenced Plot	
	1947	1958	1947	1958
(2) DICOTYLEDONS (*Continued*)				
(*a*) HERBS (*Continued*)				
Ranunculus lappaceus Sm. var. *subsericeus* Benth.	0·9	2·9	3·1	8·8
Rumex acetosella L.	+	0·5	+	0·2
Scleranthus biflorus Hk. f.	+	0·5	0·9	1·6
S. mniaroides F. Muell.	+	+	+	+
Senecio lautus Sol.	2·8	0·5	6·2	0·2
Stellaria multiflora Hook.	+	+	+	+
S. pungens Brongn.	+	+	+	+
Viola betonicifolia Sm.				
(*b*) SHRUBS				
Grevillea australis R. Br.	+	0·5	+	0·2
Hovea longifolia A. Cunn.	0·5	1·4	+	+
Hymenanthera angustifolia R. Br.	0·3	+	0·4	0·2
Kunzea muelleri Benth.	+	+	1·6	3·4
Lissanthe montana R. Br.	0·1	+	+	0·8
Olearia frostii (F. Muell.) J. H. Willis	+	+	0·3	+
O. floribunda Benth. (*O. algida* N. A. Wakefield)	—	—	+	0·2
Orites lancifolia F. Muell.	+	+	+	+
Oxylobium ellipticum R. Br.	0·1	0·3	0·1	0·2
Pimelea alpina F. Muell.	0·7	0·3	0·6	0·2
P. biflora J. H. Willis	—	+	—	—
Pleurandropsis trymalioides F. Muell.	0·5	0·5	0·8	9·2

APPENDIX II

SPECIES WHICH DO NOT OCCUR IN GRASSLAND C BUT ARE MENTIONED IN PAPERS I AND II OF THIS SERIES

Aciphylla glacialis F. Muell.
Agropyron scabrum (Lab.) Pal. Beauv.
Baeckea gunniana Schau.
Bossiaea foliosa A. Cunn.
Carex gaudichaudiana Kunth.
Claytonia australasica Hk. f.
Eucalyptus delegatensis R. T. Baker
E. pauciflora Sieb.
Ewartia nubigena Beauv.
Hypochoeris radicata L.
Pentachondra pumila R. Br.
Phebalium podocarpoides F. Muell.
Picris hieracioides L.
Prostanthera cuneata Benth.
Restio australis R. Br.
Sphagnum leionotum C. M.
Stipa nivicola J. H. Willis
Stylidium graminifolium Swartz
Themeda australis (R. Br.) Stapf

OPAL PHYTOLITHS IN SOME VICTORIAN SOILS AND "RED RAIN" RESIDUES

By G. Baker*

[*Manuscript received August* 26, 1958]

Summary

Opaline bodies in certain Victorian soils have been regarded in the past as sponge spicules. It is now shown that the majority of these opaline bodies are the same as those developed in certain plants, hence they are recorded as opal phytoliths. This corrected identification of the opaline bodies is of fundamental significance in affecting certain aspects of the interpretation of the history of such components of soils. It is no longer necessary to consider these bodies of opal as sponge spicules carried into soils by wind transportation or other means. They are released from plants containing them and shed into the soils on the decomposition, or destruction during grass and forest fires, of phytolith-bearing vegetation, or sometimes via the dung of graminiferous animals. A few smaller phytoliths do become wind-borne, as evidenced by their occurrence in "red rain" and "red snow" residues.

It is also shown that distilled water should always be used in treating soils for examination of their phytolith populations, because a small quantity of the smaller phytoliths (and diatoms) occurs in tap-water.

I. Introduction

Opal phytoliths are minute bodies of isotropic silica which have been precipitated as unwanted material or as reinforcements of cell structures in some plants, including grasses, sedges, reeds, and some woods, and hence are sometimes referred to as "plant opal" or "grass opal" bodies (Smithson 1956*b*, 1958). They become released into soils either: (i) on natural decay of the containing plant tissue (largely grass leaves), (ii) as a consequence of grass or forest fires, or (iii) via the dung of herbivorous animals, whether directly as animal droppings or by the spreading of farmyard manure.

Although they are not fine-pointed, slender bodies like most spicules they can nevertheless be regarded as "plant spicules", inasmuch as some of them perform the function of strengthening certain plant tissues.

Their microscopic shapes (in outline aspect) are many and diverse (Figs. 1–5). They include plain and ornamented straight rods, minutely denticulated, spiny, and serrated rods, sometimes tapered and curved rods, and rarely, diverging branched rods; straight tubes (rare); rectangular plates; hooked forms; spinose forms (other than rods); "chunky" forms; and examples with shapes resembling cones, spindles, boats, ovoids, spheroids, wedges, and dumbbells. Others are heart-shaped, barrel-shaped, hat-shaped, fan-shaped, flask-shaped, pear-shaped, tooth-shaped, berry-shaped, carrot-shaped, and club-shaped. A few have outlines resembling the shapes of: hatchet, hourglass, spearhead, nailhead, artefact, bobbin, capstan, funnel, tumbler, and knucklebone. Occasional specimens of the

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forms allied to dumbbells show double swellings. Some examples are pseudomorphous replacements of the cuticle of plants, and are referred to herein as cuticle replacements. Others are fragments of opaline cell-wall linings. In addition to this multiplicity of shape types, there are phytoliths for which there are no short descriptive shape terms, and such types are therefore grouped as nondescript. Several of the shape types mentioned have been illustrated by Smithson (1958, pp. 151–3 and Plate 1) for British soils and plants, and by Netolitzky (1929) and others for European and Russian soils and plants. Hat-shaped and club-shaped types have been figured by Küster (1956, pp. 506, 508).

Recently, Smithson (1958, p. 148) recorded that small bodies of opaline silica such as these were recognized as far back as 1835 by Struve, that the term "phytoliths" was applied to them by Ruprecht in 1866, and that similar opaline bodies forming the components of many plants were referred to by Grob (1896–97), Netolitzky (1929), and Prat (1931). Other authors who have referred to them include Cruger (1857), Kohl (1889), Mobius (1908*a*, 1908*b*), Molisch (1913, 1918, 1923), and Küster (1956). Smithson (1956*a*, 1956*b*, 1958) further pointed out that continued interest in these opaline bodies from plants and in soils is indicated by the works of Tyurin (1937), Usov (1943), van Rummelen (1953), Parfenova (1956), Parfenova and Yarilova (1956), and Yarilova (1956).

The nature and occurrence of phytoliths in British soils and plants have been described in recent years by Smithson (1956*a*, 1956*b*, 1958) and by Parry and Smithson (1957, 1958). Examples referred to as Kieselkörper in plant epidermis have been illustrated by Küster (1956, pp. 506–8).

The true nature of comparable bodies of opal in Australian soils was not recognized until the end of last year, when some of Dr. F. Smithson's preparations were shown to the author. Most such bodies have evidently been mistaken for sponge spicules in the past, or else overlooked, although Chapman and Grayson (1903, p. 25) referred to "numerous traces of the siliceous elements present in grasses, sedges and other plants structurally allied" among the constituents of the residue from wind-borne dust precipitated as "red rain" in February and March 1903.

Inclusions of silica in timbers have been recorded by Petrucci (1903), Gonggrijp (1932), Desch (1941), Frison (1942), Besson (1946), Amos and Dadswell (1948), and Amos (1952). These opal inclusions in the timbers have been variously called concretions, aggregates, inclusions, bodies, deposits, corpuscles, etc., but the term "phytoliths" should embrace all of these terms.

According to Smithson (1958, p. 148), the term "phytolith", implying the stony part of a plant, appears to be used only for bodies which are minute parts of the plants that secrete them. Hence it is not applied to diatom skeletons where the secretion is the full size of the organism. The term could logically be applied to any mineral substance secreted by a plant, e.g. calcium carbonate as well as opal.

As used in this paper, the term is qualified as "opal phytoliths", from which category the opaline frustules of diatoms are intentionally omitted. The science of fossil plants is sometimes referred to as "phytolithology", and the term "phytoliths" should therefore be broad enough to embrace both recent and fossil microscopic bodies of this nature (whether opaline silica or other mineral matter), if fossil examples are subsequently shown to exist.

Opal phytoliths are probably much more common and more durable than other forms of inorganic matter precipitated in plant structures. Although the shapes of a few of the opal phytoliths resemble those of some fragmented and slightly worn sponge spicules, they can be distinguished by the absence of the narrow axial canal so typical of sponge spicules.* Few sponge spicules and diatom skeletons have been detected among the assemblages of opaline silica bodies in various Victorian soils examined herein.

Phytoliths in British soils and grasses were demonstrated to the author by Dr. F. Smithson at the Agricultural Chemistry Department, University College of Wales, Bangor, during a short visit there in November 1957. Early in 1958, Associate Professor G. W. Leeper of the Agricultural Chemistry Department, University of Melbourne, suggested that the mineral grain mounts of the fine sand fractions of certain Victorian soils, prepared and described by Nicholls in 1936, should be re-examined in the light of Dr. Smithson's observations and studies. As a result, it is shown herein that most of the opaline silica bodies hitherto considered to be sponge spicules can be correlated with the phytoliths recorded from British and Russian plants and soils.

II. Material Examined

Several Victorian soils studied over 20 years ago, to determine the mineralogy of their fine sand fractions, were reported to contain sponge spicules in numbers which were higher in the surface soils, falling off with increasing depth (Leeper, Nicholls, and Wadham 1936, p. 108; Nicholls 1936, pp. 29–31; 1939). The permanent grain mounts originally utilized in these studies were re-examined and found to contain an abundance of opal phytoliths and very few actual sponge spicule fragments. The spicules were determined by Mr. F. Chapman (see Nicholls 1936, p. 33) as being from the freshwater sponge *Spongilla*, and in some samples as resembling *Spongilla cinerea* Bowerbank. The basis of this generic and specific determination could have been that *Spongilla* was the only known freshwater sponge in Victoria, and hence any spicules observed in soils in Victoria would naturally have become assigned to this genus. Otherwise it is usually regarded as impossible to determine the genera or species of detached and isolated sponge spicules (Twenhofel and Shrock 1953, p. 77), and they can rarely be classified more closely than families or suborders.

Opaline bodies have also been recorded as sponge spicules in the surface soils from many localities in Australia (Carroll 1931, pp. 132–3; 1933), and in New South Wales soils (Brewer 1955, 1956; Leeper 1955), but examples of these were not available for investigation of probable phytolith contents.

The Victorian soils now known to contain phytoliths are recorded by Leeper, Nicholls, and Wadham (1936) and Nicholls (1936) as coming from the localities listed in Table 1.

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*It has not been determined herein whether broken spicules with an axial canal represent broken sponge spicules or broken portions of silicified plant hairs.

The permanent mineral grain mounts of the fine sand fractions (0·02–0·20 mm) of most of the soils listed in Table 1, were made available through the courtesy of Professor E. S. Hills, F.R.S.; they are catalogued as Reg. Nos. 318–334 in the Mineral Grain Slide Collection, Geology Department, University of Melbourne. In addition, clove oil and refractive index liquid mounts have been examined of a sample of topsoil from the summit of Mt. Gellibrand, Western District, regarded as being among the richest of Victorian soils for its content of so-called "sponge spicules". Its fine sand and silt fractions were prepared by Associate Professor G. W. Leeper.

TABLE 1

LOCATIONS OF VICTORIAN SOILS CONTAINING PHYTOLITHS

Geological Formation	Soil Depth (in.)	Locality
Jurassic sandstones	6–12	Leongatha, South Gippsland
	4–8	Turton's Track, near Beech Forest, Otway Ranges
	0–4	Merino, Western District
	0–4	Poowong, South Gippsland
	12–15	Poowong, South Gippsland
	0–4	Strzelecki, South Gippsland
	18–24	Strzelecki, South Gippsland
Older basalt	10–20	Nilma, near Warragul, Gippsland
Newer basalt	0–8	Dixie, near Terang, Western District
	12–18	Dixie, near Terang, Western District
	27–60	Dixie, near Terang, Western District
	60–76	Dixie, near Terang, Western District
	18–40	Moyne Falls, near Macarthur, Western District
	12–24	Woorndoo, Western District
	0–3	Birregurra, Western District
	0–7	Mt. Gellibrand, between Winchelsea and Colac, Western District
Quaternary sand	4–14	Near Orbost, East Gippsland
	10–20	Wannon Falls, Western District

Two samples of "red rain" residues collected by Mr. F. Chapman at Camberwell, near Melbourne, in 1903, were also re-examined for their content of opaline silica bodies. These samples were located in the Chapman Collection of rocks and minerals (purchased by the Royal Melbourne Technical College), and donated by Mr. W. A. J. Saunders through the courtesy of Mr. T. Nicholas, for the purposes of this study. These two samples are now registered in the collection of the Melbourne University Geology Department (M.U.G.D. Reg. Nos. 3457 and 3458).

Another sample of "red rain" residue which fell in the grounds of the University of Melbourne in April 1938, and was collected on a microscope slide (M.U.G.D. Reg. No. 601, Mineral Grain Slide Collection) by the author, was investigated for its content of phytoliths, diatoms, and sponge spicules. Residue from "red snow" (M.U.G.D. Reg. No. 1110) collected by D. McCance from Mt. Feathertop, North Eastern Victoria, in August 1939 has also been examined.

Finally, a sample of Melbourne tap-water was shown to contain small amounts of opaline silica bodies in the form of diatoms, sponge spicules, and minute phytoliths, and hence this water should not be used in the preparation of samples required for studies of the opaline silica bodies in soils. The same no doubt applies to many other tap-waters, more especially at certain times of the year.

III. Opal Phytoliths in Soils

High power examination under the petrological microscope of the original permanent grain mounts of the fine sand fractions of several Victorian soils prepared by Nicholls (1936), and of the sample from Mt. Gellibrand (Leeper, Nicholls, and Wadham 1936), reveals that the greater proportion of the isotropic silica bodies present are opal phytoliths.

Their identity as opal has been confirmed from their optically isotropic character, their low refractive index ($n_{Na} = 1{\cdot}454$ to $1{\cdot}458$), and their low density (*c.* 2·15). The range of the refractive index values indicates that the water content of the opal varies from approximately 3·5 to 5 per cent. Their differentiation from fragmented or whole sponge spicules (which also consist of opaline silica) is based on: (i) the absence of the fine central canal (axial tube) which is typically present in most sponge spicules (Twenhofel and Shrock 1953, p. 77), and is described as occurring in spicules of the order Cornacuspongida (which contains the freshwater sponge family Spongillidae) in the following terms—"Alle Spicula besitzen, soweit bekannt, eine organische Grundlage, den sogenannten Achsenfaden" (Hentschel 1923–1925, p. 384); (ii) their shapes, which are characteristic and by no means to be confused with those of sponge spicules illustrated in the "Treatise on Invertebrate Paleontology" (Joint Committee on Invertebrate Palaeontology 1955) and other texts; (iii) their sculpture (or ornamentation), which is distinctive compared with the usual smoothness of many siliceous sponge spicules; (iv) the fact that they are identical in shape, size range, and general appearance (sculpture, colour variations, inclusions, etc.) with many of the phytoliths described from British soils and observed *in situ* in British plants (Smithson 1956*a*, 1956*b*, 1958; Parry and Smithson 1957, 1958), and in other plants (Netolitzky 1929; Küster 1956; etc.). Furthermore, the smaller phytoliths, some of which may be fragments of larger phytoliths, do not reveal the fine regular ornamentations possessed by complete or fragmented diatom frustules, and are never as delicate as fragments of the diatoms.

This corrected identification of the greater proportion of opaline silica bodies in the Victorian soils investigated herein, has a significant bearing upon certain aspects of the interpretation of the history of those soils. It is no longer necessary to think in terms of introducing immense numbers of wind-borne opal bodies as "sponge spicules" into soils all over Victoria, when a source for these bodies as opal phytoliths is readily to hand and available in large quantities in opal-secreting plants such as grasses and reeds, and in the wood of trees. That some released phytoliths are transported by wind currents is evidenced by their detection in "red rain" and "red snow" residues, but their original source as bodies of opal lies in phytolith-bearing plants.

Opal phytoliths are not confined to the smaller particles of the fine sand fractions (0·02–0·20 mm) of the soils. Smithson (1958, p. 149) has shown that in some of the British soils they occur also among the larger particles of the silt fraction (0·002–0·020 mm). They have also been detected in the silt fraction of the topsoil from Mt. Gellibrand, western Victoria, and from Dalmore, Koo-wee-rup Swamp, south Gippsland. Several of silt size have been observed in the wind-borne dusts precipitated with rain or snow. It is thus obvious that a representative concentrate of the phytoliths in soils has to be obtained by selecting non-standard size limits to cover this size range.

IV. Assemblages of Opal Phytoliths

Since microscopic examination of the content of opaline silica bodies in the Victorian soils listed in Table 1 has revealed that sponge spicules are very rare (none in many slides, one in each of a few slides, and a maximum of three in one slide), the frequency figures listed by Nicholls (1936, p. 31) for "sponge spicules" can thus be taken to represent a close approximation of the "phytolith" contents of the fine sand fractions. The relevant sections of Nicholls's table pertaining to these bodies of opaline silica are reproduced in Table 2.

In descriptions of the phytoliths the term "sculpture" refers to minute surface features such as low ridge-like projections, serrations, rounded protuberances, crenulations, irregular facets, depressions, and small pits. These features are seldom regular on any one phytolith, and they combine to impart a marked rugose character to the surfaces of many phytoliths, but some examples are relatively smooth.

The majority of the phytoliths are almost colourless; some reveal a faint pinkish brown cast, a few are light or darker brown, while rare examples are partially opaque. In reflected light, opaque portions, the nature of which remains undetermined, are invariably light grey to whitish in colour.

Rod-like phytoliths are usually though not always the most common types encountered in the various assemblages. They show considerable variation in character, some appearing smooth, some "prickly", and others serrated, unevenly crenulated, or irregularly embayed, etc. Many of these features are original to the phytoliths but some of the embayments may have resulted from corrosion in the soil. The different varieties of rods and the many other shape types (Figs. 1–5) of the phytoliths combine to form somewhat different assemblages. Although the various assemblages have certain characteristics in common, no two are quite identical, whether from the soils on similar rocks in different localities or from different depths in a soil profile at any one locality. On the other hand, some of the phytolith assemblages of comparable character are rather distinctive from the general run of assemblages. Two such assemblages are from: (i) 4–8 in., Turton's Track, near Beech Forest, Otway Ranges, and (ii) 10–20 in., Nilma, near Warragul, Gippsland—in both of which the irregularly berry-shaped types of phytoliths are either dominant or important, while most other types are relatively rare. The dominance of any particular phytolith shape type in the phytolith assemblages of soils is evidently a reflection of a locally dominant plant or group of plants supplying the phytoliths to the soils. It may be significant that the two comparable and distinctive phytolith assemblages from Turton's Track and Nilma, separated by approximately 140 miles, should both occur in soils on forested terrains. On the other hand, regions of similar forest, cleared no more than 50 years ago for grass, occur at Leongatha, Poowong, and Strzelecki, and the phytolith assemblages of the soils from these localities do not reveal a preponderance of berry-shaped phytoliths, although a few are present.

TABLE 2

NUMBER OF "SPONGE SPICULES" (PHYTOLITHS) PER 500 GRAINS* IN THE FINE SAND FRACTIONS OF VARIOUS VICTORIAN SOILS

Soil No.	Locality	Soil Depth (in.)	Fine Sand Fraction in Soil (%)	Number of Phytoliths† per 500 Grains
1	Leongatha, South Gippsland	9–18	40	9
2	Turton's Track, near Beech Forest, Otway Ranges	4–8	15	4
3	Merino, Western District	0–4	35	32
4	Poowong, South Gippsland	0–4	44	11
5	Poowong, South Gippsland	12–15	44	11
6	Strzelecki, South Gippsland	0–4	26	4
7	Strzelecki, South Gippsland	18–24	27	7
8	Wannon Falls, Western District	10–20	32	—‡
9	Near Orbost, East Gippsland	4–14	28	7
10	Woorndoo, Western District	12–24	9	—‡
11	Moyne Falls, near Macarthur, Western District	18–40	5	6
12	Dixie, near Terang, Western District	0–8	49	25
13	Dixie, near Terang, Western District	12–18	38	12
14	Dixie, near Terang, Western District	27–60	20	2
15	Dixie, near Terang, Western District	60–76	15	2
16	Nilma, Gippsland	10–20	21	6
17	Birregurra, Western District	0–3	27	5

*Counted by Nicholls (1936, p. 31).

†Most opaline bodies counted originally as "sponge spicules" are in reality phytoliths ("plant spicules"), so the figures in the last column are close to the true number for phytoliths.

‡Although not encountered in the "500 grain count" by Nicholls, phytoliths have been detected in the permanent grain mounts of samples Nos. 8 and 10.

A wide range of individual phytolith shapes are depicted in the accompanying sketches (Figs. 1–5). These have been selected from the assemblages in order: (*a*) to provide some conception of the variety and complexity of shapes represented;

(*b*) to provide an overall picture of the general nature of the several phytolith assemblages encountered in different soils; (*c*) to indicate that there are certain marked variations from some assemblages to others. The peculiarities of shape or ornamentations, or both, of phytoliths from the soils should help in their recognition in any particular plant or group of plants (especially grasses and trees) which is phytolith-bearing. Comparison of a phytolith assemblage in a soil with that in plants could indicate the general nature of a community of phytolith-bearing plants supported on particular soils at various sites, provided that other factors (excessive wind erosion etc.) have not upset the balance.

The diagrams (Figs. 1–5) represent outline sketches only of the phytoliths as they appeared (mainly in permanent mounts) under magnifications of ×360. A few sculptural elements have been added to some of the sketches. The opaline bodies were conspicuous compared with dominant quartz in the soil fractions, since the permanent mounting medium used was Canada balsam, with a refractive index of approximately 1·54 (close to that of quartz); under these conditions the quartz was relatively inconspicuous in transmitted light. Fractions not examined in permanent mounts (e.g. the Mt. Gellibrand examples, the "red rain" residues, and the "red snow" residues) were examined in clove oil of refractive index approximately 1·53, with similar effects. Each of the phytoliths sketched in Figures 1–5 was checked for isotropism.

All of the opaline bodies depicted in Figures 1–5 cannot definitely be proved to have come from phytolith-bearing plants, because no detailed investigations have yet been conducted into the nature and shapes of opal phytoliths in Victorian plants. Nevertheless, the published evidence (Netolitzky 1929; Smithson 1956*a*, 1956*b*, 1958; Parry and Smithson 1957, 1958; etc.) points to the strong probability of all of them being phytoliths; this is supported to some extent by the fact that in one of the permanent grain mounts (from 60–76 in., Dixie, Western District), seven phytoliths resembling others in the assemblages from the soils have been detected *in situ* in two fragments of plant tissue.

It is at present difficult to assess the nature of shape changes that may have occurred as a consequence of attrition or corrosion of the phytoliths in the Victorian soils examined, since their first release as individual bodies from the host plants. The general appearance of most phytoliths suggests little or no fundamental change in shape except for some fracturing, and occasional modification to a minor degree by corrosion in the soils, while some phytoliths in wind-borne dusts seem to have been little more affected.

Practically all of the assemblages examined contain one or more examples of cuticle replacement by opaline silica. Some of these have evidently been fractured from rather larger pieces; they are classified as phytoliths, however, inasmuch as they represent only minute parts of the silica-secreting plant organisms.

The following are brief descriptions of the characteristics of the opal phytoliths determined in the soils listed in Table 1. Many more complexities are present than can be covered in a limited space.

(*a*) *Leongatha, South Gippsland*

(i) 6–12 *Inches.*—Opal phytoliths are relatively common (Fig. 1, Nos. 26–49), largely colourless, sometimes light to dark brown and translucent, and occasionally subtranslucent to almost opaque and brownish. The brown colour, as in other assemblages, is evidently original to the phytoliths since the treatment of the soil sample was such as to remove thin films of adventitious mineral matter.

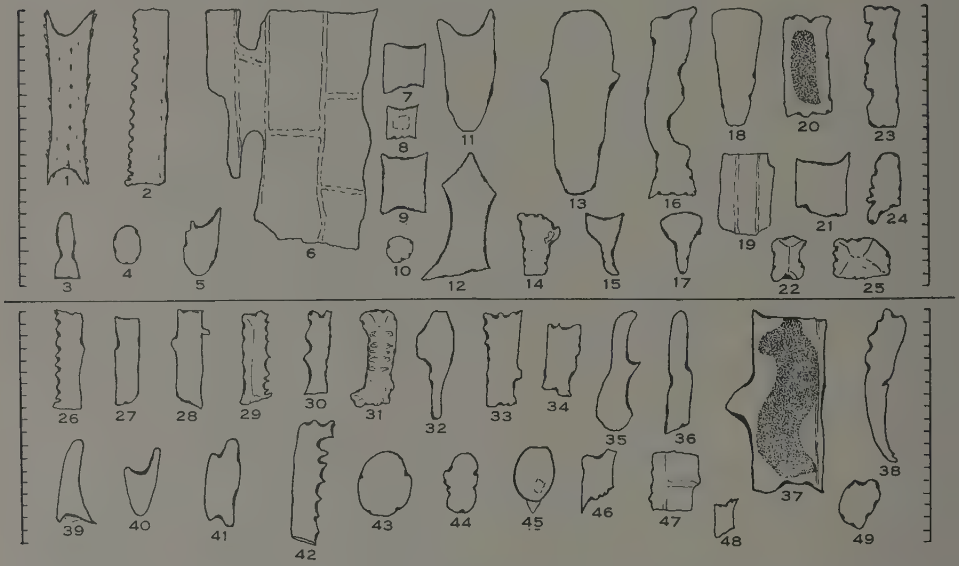

Fig. 1.—Outline sketches of opal phytoliths in some Victorian soils. Nos. 1–25, from 0–7 in., summit of Mt. Gellibrand, between Winchelsea and Colac, Western District. Nos. 26–49, from 6–12 in., Leongatha, South Gippsland. Each scale graduation represents 0·010 mm.

Some of the phytoliths reveal a faint milkiness (milky opal), others are water-clear and colourless (hyalite variety of opal); examples with included opaque matter are relatively rare (Fig. 1, No. 37).

Many of the phytoliths are rods with long, approximately rectangular outlines (Fig. 1, Nos. 27–34), which vary in length from 0·04 to 0·14 mm and average 0·02 mm in width, while their thickness ranges from 0·01 to 0·02 mm. One—sometimes both—of the longer, more or less parallel edges of these rods is sometimes smooth, but often wavy in outline. Occasionally one long edge shows minute tooth-like protuberances resembling a saw-edge where approximately regular, the other edge is more or less smooth (Fig. 1, No. 26); others have a few spine-like outgrowths (Fig. 1, No. 28), and some are "prickly". Low ridges trend along the length of a few of the rods (Fig. 1, No. 29); some are rugose (Fig. 1, No. 31); rare examples are curved and tapering (Fig. 1, No. 38).

Among the less common shape types, berry-like examples (Fig. 1, No. 43) are the next most abundant to rods. A few others are irregularly subspheroidal and 0·05 mm in diameter. Some tend to be hooked, a few are "chunky", while several are of nondescript shape. Examples of cuticle replacements are represented by flat plates of opaline silica with regularly arranged ridges (Fig. 1, No. 47). No fragments of sponge spicules were observed.

(b) *Turton's Track, near Beech Forest, Otway Ranges*

(i) 4–8 *Inches.*—Phytoliths are uncommon (Fig. 4, Nos. 1–6). Irregularly berry-shaped examples (Fig. 4, No. 5) up to 0·06 mm across dominate the sparse assemblage of phytoliths, being more common than rods (Fig. 4, Nos. 3, 4). In this respect the phytolith assemblage is significantly different from most others described herein. It bears a close resemblance to the assemblage from Nilma, near Warragul, Gippsland, which comes from a similar terrain of forested soils (or soils heavily forested prior to clearing). The assemblage points to derivation from a phytolith-bearing plant host, or group of such plants (possibly trees) which are more dominant than in other terrains covered by the present investigations.

One hat-shaped phytolith (Fig. 4, No. 6) was observed. One (rod-shaped), which appeared to have a central canal under low magnifications and might thus be taken to represent a sponge spicule fragment, was observed under higher magnifications to be a phytolith with a low ridge on its upper surface as exposed in the permanent mount. No true sponge spicules were detected.

(c) *Merino, Western District*

(i) 0–4 *Inches.*—Only one sponge spicule fragment was observed in the whole of the mineral grain mount, but phytoliths are common (Fig. 2, Nos. 1–26), several being water-clear and colourless. The largest rod is 0·40 mm long and 0·04 mm wide—the largest seen in any of the assemblages. A few rods are smooth (Fig. 2, No. 4), one or two are ridged (Fig. 2, No. 3), and others reveal well-developed serrations along both of the longer sides (Fig. 2, No. 2); tooth-shaped protuberances are often more marked, more numerous, and often sharper on one of the longer sides than on the other. Occasional rods contain an opaque whitish, internal cloud-like aggregate of included matter arranged as indicated in Figure 2, No. 6.

Hat-shaped (Fig. 2, No. 10), dumbbell-shaped (Fig. 2, No. 25), heart-shaped (Fig. 2, No. 24), hook-like (Fig. 2, No. 15), flask-shaped (Fig. 2, No. 23), barrel-shaped, and berry-like (Fig. 2, No. 17) forms, several other shapes, and occasional "chunky" forms are also present. Some of the smaller rod-like examples are probably broken from longer rods, but several of these may represent casts of short rectangular plant cells.

(d) *Poowong, South Gippsland*

(i) 0–4 *Inches.*—Only one sponge spicule fragment and a few phytoliths (Fig. 4, Nos. 7–15) are present. The most frequent phytoliths are rods (Fig. 4, Nos. 7, 8) with roughly rectangular outlines. The largest rod is 0·30 mm long and 0·025 mm wide. Occasional specimens of the phytoliths are pointed pear-shaped bodies 0·10 mm long (Fig. 4, No. 11), approximately flask-shaped (Fig. 4, No. 9), fan-shaped (Fig. 4, No. 15), or knobbed (Fig. 4, No. 12), etc. A few small "chunky" phytoliths and rare cuticle replacements also occur.

(ii) 12–15 *Inches*.—At this depth a similar quantity of phytoliths to that from the topsoil (see 0–4 in. sample, above) is present, with the characteristic shape types represented by examples sketched in Figure 4, Nos. 30–37. Rare examples are peg-like (Fig. 4, No. 33), hatchet-shaped (Fig. 4, No. 37), or show double swellings (Fig. 4, No. 36). The largest rod is 0·20 mm long and 0·025 mm wide. No sponge spicule fragments were detected.

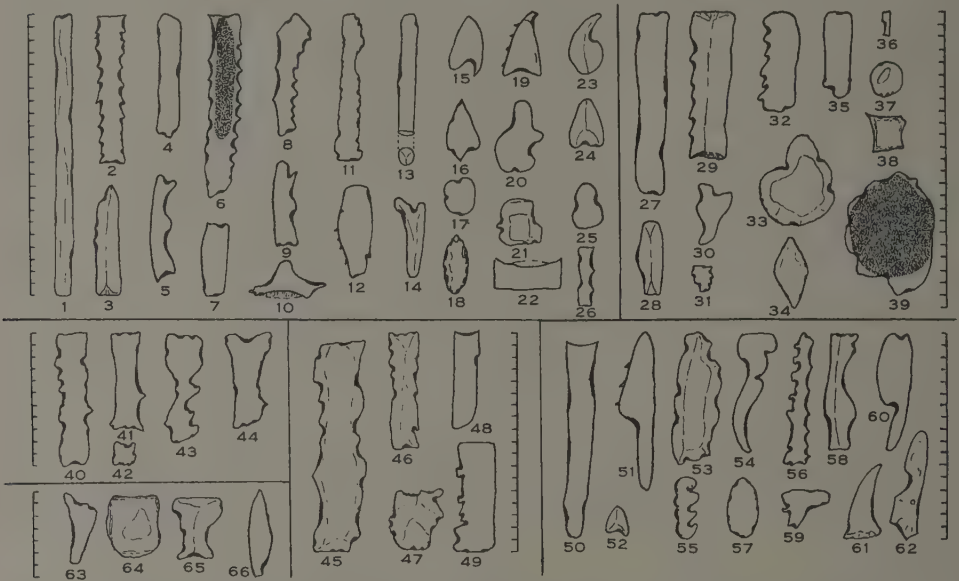

Fig. 2.—Outline sketches of opal phytoliths in some Victorian soils. Nos. 1–26, from 0–4 in., Merino, Western District. Nos. 27–39, from 4–14 in., near Orbost, East Gippsland. Nos. 40–44, from 12–24 in., near Woorndoo, Western District. Nos. 45–49, from 18–40 in., Moyne Falls, near Macarthur, Western District. Nos. 50–66, from 0–8 in., Dixie, near Terang, Western District. Each scale graduation represents 0·010 mm.

(*e*) *Strzelecki, South Gippsland*

(i) 0–4 *Inches*.—Several types of phytoliths (Fig. 4, Nos. 16–29), three sponge spicule fragments, and one fragment of a diatom frustule are present. Typical rod-like phytoliths (Fig. 4, Nos. 16–18) are the most frequent of the shape types. One or two of the rods are curved and show a low ridge (Fig. 4, No. 26). Irregular "chunky" forms also occasionally possess low ridges (Fig. 4, Nos. 23, 24). Among the other shapes represented are elongated ovals (Fig. 4, Nos. 19, 21, 29) occasionally ornamented with a low ridge, and rare elongated heart-shaped bodies (Fig. 4, No. 28).

(ii) 18–24 *Inches*.—Phytoliths (Fig. 4, Nos. 38–47) are principally rods, occasionally with crenulate edges (Fig. 4, No. 43), sometimes with a low ridge (Fig. 4, No. 39). A few are smooth but most are minutely rugose, their sculpture patterns being accentuated under certain illuminations. A few are brownish in colour, but the majority, as in all other assemblages, show a faint pinkish cast. Only one sponge spicule fragment was detected.

Compared with the topsoil sample (see 0-4 in. sample, above), shape variations among the phytoliths are mainly only evident among the more rare (i.e. non-rod-shaped) types.

(*f*) *Nilma, near Warragul, Gippsland*

(i) 10–20 *Inches*.—No sponge spicules were detected, and the opal phytoliths (Fig. 3, Nos. 18–29) are relatively few in number and somewhat varied in shape. Several consist of the usual finely sculptured rods (Fig. 3, Nos. 18, 19), some are curved and occasionally have a low ridge (Fig. 3, No. 20), and one or two tend to be elongated wedge-shaped bodies. The largest rod present is relatively smooth, 0·110 mm long and 0·025 mm wide.

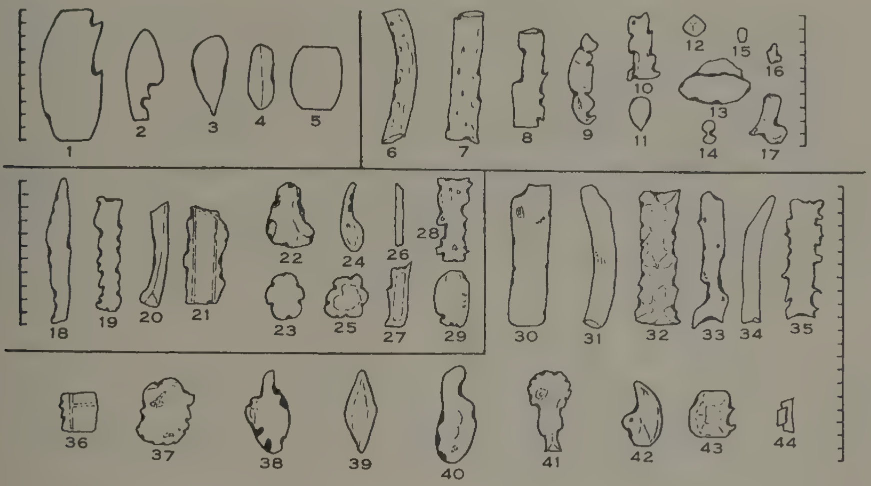

Fig. 3.—Outline sketches of opal phytoliths in some Victorian soils. Nos. 1–5, from 12–18 in., Dixie, near Terang, Western District. Nos. 6–17, from 60–76 in., Dixie, near Terang, Western District. Nos. 18–29, from 10–20 in., Nilma, near Warragul, Gippsland. Nos. 30–44, from 0–3 in., Birregurra, Western District. Each scale graduation represents 0·010 mm.

Irregularly berry-shaped phytoliths (Fig. 3, Nos. 23, 25) are the next most common to the rods, and occur in approximately the same quantities as in the assemblage from Turton's Track (Section IV(*b*)). Other types present are rare flask-shaped examples (Fig. 3, No. 24), a few "chunky" types (Fig. 3, No. 22), and occasional thin plates with ridges (Fig. 3, No. 21), which represent cuticle replacements.

(*g*) *Dixie, near Terang, Western District*

(i) 0–8 *Inches*.—Phytoliths are common (Fig. 2, Nos. 50–66), and the assemblage is dominated by rods, most of which are finely sculptured. The largest rod is 0·275 mm long and 0·020 mm wide. Some rods are deeply denticulate to spinose (Fig. 2, No. 56), some show rather more rounded crenulations (Fig. 2, No. 55). Other types are occasional "chunky" forms, cuticle replacements (Fig. 2, No. 64), and a few forms which are heart-shaped (Fig. 2, No. 52), club-shaped (Fig. 2, Nos. 51, 60), spearhead-shaped (Fig. 2, No. 66), and tooth-shaped (Fig. 2, No. 61). Several have nondescript shapes (Fig. 2, Nos. 53, 54, 59, 62, and 63).

Where exposed obliquely end on in the permanent mount, some rods reveal shallow concave end surfaces; but in other assemblages a few similarly mounted examples show end surfaces with convexly raised regions with triangular facets (Fig. 2, No. 13), resulting from the presence of three diverging low ridges. Only one irregularly berry-shaped form was observed.

Detailed examination of the whole grain mount revealed only one fragment of a sponge spicule.

(ii) 12–18 *Inches*.—Phytoliths (Fig. 3, Nos. 1–5) are again typically finely sculptured rods, of which a few are spinose and one is slightly tapered. The largest rod is 0·225 mm long and 0·035 mm wide. "Chunky" forms are relatively common. Two of the phytoliths are small barrel-shaped forms (Fig. 3, No. 5), one is top-shaped (Fig. 3, No. 3), an oval form possesses a low ridge (Fig. 3, No. 4), and a few are nondescript in shape (Fig. 3, Nos. 1, 2). Rare cuticle replacements also occur. No sponge spicules were detected.

(iii) 27–60 *Inches*.—Typical, finely sculptured rods dominate an assemblage in which phytoliths are rather rare and sponge spicules absent. The largest rod is 0·210 mm long and 0·025 mm wide. No phytolith shapes other than the rods and rare "chunky" forms are present.

(iv) 60–76 *Inches*.—Phytoliths (Fig. 3, Nos. 6–17) are not common, and again consist chiefly of the usual types of rods (Fig. 3, No. 7). No sponge spicule fragments are present. Compared with the sample from 27–60 in. (see above), however, a greater variety of shapes is present. The largest rod is 0·100 mm long and 0·020 mm wide. One is curved (Fig. 3, No. 6) and finely ornamented, another is serrated (Fig. 3, No. 8). Types other than the rods are hat-shaped (Fig. 3, No. 13), top-like (Fig. 3, No. 11), or nondescript (Fig. 3, Nos. 9, 17).

Of especial interest is the occurrence in the permanent grain mount of two fragments of plant tissue containing opal phytoliths still *in situ*. One fragment possesses five phytoliths, one of which is irregularly club-shaped, embayed, and 0·110 mm long by 0·030 mm wide. Another is dumbbell-shaped (Fig. 3, No. 14), one is oval (Fig. 3, No. 15), one is a small "chunky" phytolith (Fig. 3, No. 16), and one is a small, narrow, elongated oval body drawn out at one end. In the second plant fragment a finely sculptured rod-like phytolith, 0·075 mm long and 0·025 mm wide, occupies the full width of an elongated plant cell, but not its full length, since a distance of 0·025 mm at each end of the rod is unoccupied cell. This shows that rod-like phytoliths are precipitated within the cell walls of plant tissue, like the dumbbell and other shape types figured by Smithson (1958, Plate 1) and Netolitzky (1929). Such bodies thus contrast with the less common cuticle replacement type of phytolith, where opaline silica has replaced cuticle rather than forming casts by infilling cell structures or by growing as smaller bodies in the lumen.

(*h*) *Moyne Falls, near Macarthur, Western District*

(i) 18–40 *Inches*.—The phytoliths (Fig. 2, Nos. 45–49) consist of occasional sculptured and sometimes wavy-edged rods (Fig. 2, Nos. 45, 46, 49) up to 0·170 mm long and 0·035 mm wide, smoother rods (Fig. 2, No. 48) 0·075 mm long and 0·025 mm wide, and one or two "chunky" forms (Fig. 2, No. 47). Rods again dominate the phytolith assemblage. Only one sponge spicule fragment was detected.

(*i*) *Woorndoo, Western District*

(i) 12–24 *Inches*.—Opaline bodies originally regarded as "sponge spicules" were not recorded by Nicholls (1936, p. 31) since they did not enter into the "500 grain count" of the fine sand fraction of this sample. Detailed examination of the whole grain mount, comprising some 1500–2000 grains, reveals only eight phytoliths. The majority are approximately rod-like (Fig. 2, Nos. 40–44) but generally rather irregularly crenulated (Fig. 2, No. 43). A few are smoother in outline (Fig. 2, No. 41) with an occasional spinose outgrowth, but all show some ornamentations. The largest rod has crenulate outlines and is 0·110 mm long by 0·025 mm wide (Fig. 2, No. 40). Smaller examples (Fig. 2, No. 42) are probably broken, corroded fragments of longer rods. No fragments of sponge spicules were detected.

(*j*) *Birregurra, Western District*

(i) 0–3 *Inches*.—Phytoliths (Fig. 3, Nos. 30–44) are dominantly rod-like; some are spinose (Fig. 3, No. 35), some smooth-walled and tapering (Fig. 3, Nos. 31, 34) and up to 0·175 mm long and 0·025 mm wide. Rare forms reveal a reticulating network of low ridges (Fig. 3, No. 32). Variations in the shapes of the rarer types of phytoliths are shown in Figure 3, Nos. 36–44. One of these is spindle-shaped (Fig. 3, No. 39), another irregularly club-shaped (Fig. 3, No. 41), and others are nondescript (Fig. 3, Nos. 37, 38, 40, 42, and 43). A few "chunky" types are present. Occasional cuticle replacements occur as flat plates with ridges (Fig. 3, No. 36) and as rare angle-pieces (Fig. 3, No. 44). No sponge spicule fragments were detected.

(*k*) *Summit of Mt. Gellibrand, between Winchelsea and Colac, Western District*

(i) 0–7 *Inches*.—Very abundant phytoliths (Fig. 1, Nos. 1–25) occur in this top-soil, and reveal a multiplicity of shape types, among which rod-like forms predominate. They constitute approximately 10 per cent. of the fine sand fraction. A few are brownish in colour but most are colourless or have a faint pinkish cast. Only two fragments of sponge spicules were observed.

The rod-like phytoliths are largely finely sculptured, sometimes plain or serrated on one side (Fig. 1, No. 2), somewhat irregular on both sides (Fig. 1, Nos. 16, 23, 24), or spiny along the longer edges and concave at the ends (Fig. 1, No. 1). Sometimes the plainer rods contain a more or less centrally disposed cloudy accumulation of undetermined opaque matter (Fig. 1, No. 20). The average size of the rods is 0·08 mm long and 0·02 mm wide, and some are only 0·005 mm thick. The largest rod in the assemblage is 0·20 mm long and 0·025 mm wide, with the thickness practically the same as the width. As determined by rolling over in the refractive index liquid mount and measuring with an eyepiece scale, most rods are more or less equidimensional normal to the long axis; some, however, were observed to be wedge-shaped along their length.

Relatively large, thin, flat plates of opaline silica with regularly arranged low ridges (Fig. 1, No. 6) represent cuticle replacements, while smaller, square, thin plates (Fig. 1, No. 8), usually outlined by low ridges of opal, evidently represent replacements or casts of the walls of single cells. A few of the cuticle replacements preserve the outlines of the irregularly crenulate margins of the epidermal cells of grasses.

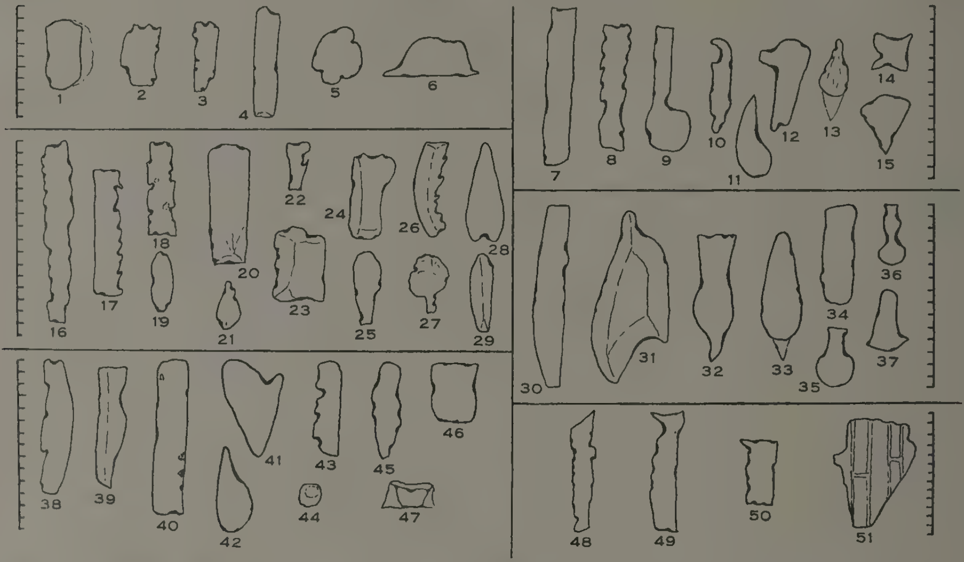

Fig. 4.—Outline sketches of opal phytoliths in some Victorian soils. Nos. 1–6, from 4–8 in., Turton's Track, near Beech Forest, Otway Ranges. Nos. 7–15, from 0–4 in., Poowong, South Gippsland. Nos. 16–29, from 0–4 in., Strzelecki, South Gippsland. Nos. 30–37, from 12–15 in., Poowong, South Gippsland. Nos. 38–47, from 18–24 in., Strzelecki, South Gippsland. Nos. 48–51, from 10–20 in., Wannon Falls, Western District. Each scale graduation represents 0·010 mm.

Other shape types present include phytoliths which are funnel-shaped (Fig. 1, No. 15), top-shaped (Fig. 1, No. 17), carrot-shaped (Fig. 1, No. 18), irregularly berry-shaped (Fig. 1, Nos. 4, 10), capstan-shaped (Fig. 1, No. 3), or nondescript in shape (Fig. 1, Nos. 5, 11–14), while a few are "chunky" with low ridges (Fig. 1, No. 25).

(*l*) *Near Orbost, East Gippsland*

(i) 4–14 *Inches.*—The phytolith assemblage (Fig. 2, Nos. 27–39) typically contains a few rods (Fig. 2, Nos. 27–29, 32, 35), some of which are occasionally serrated on one side and slightly crenulated on the other (Fig. 2, Nos. 29, 32). The largest rod is 0·150 mm long and 0·025 mm wide, and is relatively smooth and plain (Fig. 2, No. 27). Small pieces (Fig. 2, Nos. 31, 36) are evidently fragments of longer rods. A few "chunky" forms and cuticle replacements occur (Fig. 2, No. 38). One of the irregularly shaped phytoliths (Fig. 2, No. 39) is almost opaque throughout from included matter. One rare, rounded form (Fig. 2, No. 37) reveals a flattened spot on one face; this probably represents a plane of attachment to another phytolith or to an opaline cell wall lining. A few minute slivers of opal 0·015 mm by 0·005 mm in size have apparently been broken from cuticle replacement structures, and are distinguished from broken fragments of diatoms by the absence of regular ornamentations. One of the phytoliths is spindle-shaped (Fig. 2, No. 34), and some are nondescript (e.g. Fig. 2, No. 30). No sponge spicule fragments were detected.

(*m*) *Wannon Falls, Western District*

(i) 10–20 *Inches*.—The grains in this fraction are rather coarser than in the other fine sand fractions examined, and the sample was reported to contain no "sponge spicules" in a 500 grain count (Nicholls 1936, p. 31). However, seven phytoliths have been observed in the complete grain mount of some 1500–2000 particles (Fig. 4, Nos. 48–51). Most of these are the usual rods (Fig. 4, Nos. 48–50), while one is a flat, thin plate revealing cell wall casts (Fig. 4, No. 51). The rods occur in the proportion of 3 to 1 of other phytolith shapes. The largest rod is 0·125 mm long by 0·030 mm wide, while the smallest is 0·050 mm long by 0·020 mm wide. No fragments of sponge spicules were seen.

V. OPAL PHYTOLITHS IN "RED RAIN" AND "RED SNOW" RESIDUES

(*a*) *"Red Rain" Residues*

Residues from "red rain" which fell at Camberwell, near Melbourne, on February 14 and March 28, 1903, were examined by Chapman and Grayson (1903); a weight of 17 gr of dry sediment was obtained by Mr. F. Chapman from 5 fluid oz of "red rain". Seventeen different minerals were recognized in the two residues, along with numerous pieces of vegetable tissue, pollen grains, spore-like bodies, freshwater diatoms, and sponge spicule fragments, an insect wing, and, most important of all for this study of phytoliths, "*numerous traces of the siliceous elements present in grasses, sedges and other plants structurally allied*".

The original slides were not available for re-examination, but portions of these two "red rain" residues (M.U.G.D. Reg. Nos. 3457 and 3458) were immersed in clove oil (R.I. = *c*. 1·53) and other refractive index liquids and investigated under the high powers of the petrological microscope. Among the abundant organic and mineral particles constituting the greater part of the residue from the "red rain" which fell on February 14, 1903, phytoliths, diatoms, and sponge spicule fragments were detected in the proportions shown in Table 3 (as determined by particle count).

The size range of the various particles in the grain mount of this "red rain" residue is of the order of 0·0005–0·100 mm.

The phytoliths detected in the residues from both the "red rain" falls are comparable with those observed in British soils and plants and in Victorian soils, although the shapes of some seem to have been rather modified (by attrition or corrosion or both). Their average size of 0·03–0·04 mm long and 0·01–0·02 mm wide, however, is less than that of phytoliths in the fine sand fractions of the Victorian soils examined herein, where the average size is approximately 0·08 mm long by 0·02 mm wide. Their size in the "red rain" residues is more nearly that of phytoliths in the silt fractions of soils.

Their colour varies from colourless to brownish, as in examples observed in Victorian soils. The multiplicity of their shape types is indicated by Figure 5, Nos. 1–45, and there are many more than those illustrated. The great variety of forms present points to an obvious derivation from several sources.

TABLE 3

PROPORTIONS OF OPALINE SILICA BODIES COMPARED WITH OTHER CONSTITUENTS IN "RED RAIN" RESIDUE

"Red rain" fell on February 14, 1903

Particles	Percentage of Total
Phytoliths	0·65
Diatoms	0·58
Sponge spicules	0·06
Pollen grains and spores	2·00
Mineral grains, particles of plant tissue, resin bodies, etc.	96·71
Total	100·00
Number of particles counted	1546

Many of the forms depicted in Figure 5 reveal rather more complex outlines when viewed in positions at right angles. For example, the form shown in Figure 5, No. 33, is an edge-on view of forms which have dumbbell-shaped (Fig. 5, Nos. 24, 30) outlines, while the one shown by Figure 5, No. 21, is a boat-shaped side aspect of a more or less oval-shaped phytolith. Other right-angle aspects are indicated in Figure 5 (see Nos. 10, 12, 14, 18–20, 40, and 45), side by side with the aspect presented by the phytoliths in their stable positions of rest in the mounting medium.

Phytoliths of similar size and general nature have also been observed in the residue from drops of "red rain" which fell in the grounds of the University of Melbourne in April 1938 (M.U.G.D. Reg. No. 601, Mineral Grain Slide Collection). Most of the phytoliths in this sample consist of small rods, the largest of which measures 0·075 mm long by 0·010 mm wide. The rods are mainly smooth to finely sculptured, occasionally with wavy edges (sharp, rounded, or both), and one or two are tapered. Other forms of phytoliths present, averaging approximately 0·020 mm in length, are dumbbell-shaped, hook-like, flask-shaped, oval, irregular, etc., as depicted in Figure 5, and a few thin plates with ridges represent cuticle replacements.

(*b*) "*Red Snow*" *Residues*

In the residue obtained by Mr. D. McCance from a quart of "red snow" which fell on Mt. Feathertop, North Eastern Victoria, on the night of August 31, 1929 (M.U.G.D. Reg. No. 1110), a number of small phytoliths are readily recognizable among the usual assemblage of pollen grains, fragments of plant tissue, etc., mineral particles (quartz, tourmaline, felspar, etc.), and diatom frustules.

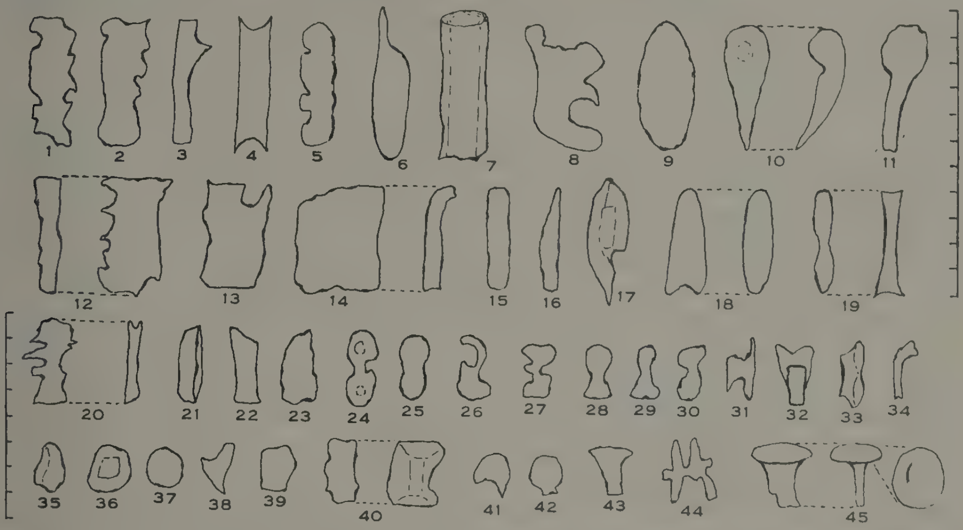

Fig. 5.—Outline sketches of opal phytoliths in "red rain" residues. Nos. 1–45, from residue collected by Mr. F. Chapman from "red rain" which fell at Camberwell, near Melbourne, on March 28, 1903. Each scale graduation represents 0·010 mm.

The phytoliths are just as small but not quite as frequent as in the "red rain" residues, and do not show as wide a range of shape types. This probably points to the finer constituents of wind-borne dust having remained suspended longer, perhaps at higher altitudes, until ultimate precipitation with the snowfall.

Among the phytolith shapes observed are: (i) rods with smooth sides, 0·025 mm long by 0·008 mm wide, (ii) rods with wavy edges, up to 0·150 mm long by 0·010 mm wide, (iii) rods ornamented with a low ridge trending along the length of the form, 0·050 mm long by 0·020 mm wide, (iv) an irregularly oval-shaped form, 0·025 mm long by 0·010 mm wide, (v) a peg-shaped form, 0·030 mm long, (vi) dumbbell-shaped forms, up to 0·015 mm long, (vii) an elongated barrel-shaped form, 0·050 mm long by 0·025 mm wide, (viii) a hat-shaped form, 0·010 mm across, and other forms.

VI. OPALINE BODIES IN MELBOURNE TAP-WATER

Because only a few diatom frustules and sponge spicules were observed in the fine sand fractions of the Victorian soils examined herein, the possibility was investigated that the few present were due to contamination by the tap-water used for particle dispersion in the soil treatment.

To test this, Melbourne tap-water was allowed to drip for nearly 5 days (June 19–23, 1958) through a 32·0 cm filter paper (ash content, 0·0049 g). After ignition of the filter paper, examination of the residue (most of which was gelatinous iron oxide) at a magnification of ×360 revealed several bodies of opaline silica. The most common are diatom frustules, of which five or six different species are represented. In addition to a few angular mineral particles up to 0·030 mm across, and one or two fine sponge spicules (fragments), several opal phytoliths were also detected. The phytoliths are mainly small rod-like forms up to 0·025 mm long, and a number are of irregular shape.

The test suffices to indicate that some degree of soil sample contamination can occur by the introduction of opaline silica bodies from tap-water. Although not serious enough to affect the main outcome of the phytolith assemblage comparisons of the fine sand fractions prepared over 20 years ago from the soils examined by Nicholls (1936), precautions were nevertheless taken to ensure no contamination of the Mt. Gellibrand fractions, or of the "red rain" residues and "red snow" residues, by using distilled water in sample preparation. The precaution becomes more necessary when investigating fine silt fractions of soils and the fine constituents of "red rain" and "red snow" residues, where opaline silica bodies such as phytoliths, diatoms, and sponge spicules are equivalent in size to those detected in tap-water, and generally smaller than those observed in the fine sand fractions of soils.

Confirmation of the possibility of contamination from tap-water is provided by the observations of Dr. A. B. Edwards, who carried out a similar test of Melbourne tap-water in March 1935 and likewise discovered a number of diatom skeletons in the residue (personal communication, 1958).

It is apparent that contamination in this way could be a far more serious problem in seasons when diatoms flourish more prolifically, or at times of the year when phytoliths are more abundantly released from the host plants and swept into large reservoirs of water by the agency of wind or by water run-off; a number may be added more directly from phytolith-bearing reeds and sedges fringing the reservoirs.

VII. Remarks and Conclusions

The minute opaline silica bodies in the fine sand (0·02–0·20 mm) and silt (0·002–0·020 mm) fractions of various Victorian soils have been shown to consist largely of phytoliths, and not sponge spicules as was originally believed. The phytoliths occur in the soils in quantities amounting usually to 1 or 2 per cent. of the whole soil, but may rise to approximately 2·5 per cent. of certain topsoils such as that from the summit of Mt. Gellibrand.

The determination of these bodies as phytoliths, in the light of recent research work overseas (Smithson 1956*a*, 1956*b*, 1958; Parry and Smithson 1957, 1958), is of fundamental significance in explaining their distribution throughout the soils of Victoria.

On the basis of their previous determination as "sponge spicules", it became necessary to postulate widespread occurrence by dispersal through aerial agencies, or by the former existence of many freshwater lakes in which sponge spicules could be generated in colossal numbers. A source, or a multitude of sources, where fresh-water sponges grew in great profusion was thus required in order to supply the immense numbers of so-called "sponge spicules" in the proportions in which these opaline bodies must obviously be represented in soils generally throughout Victoria.

On the basis of their determination as "phytoliths", which are common in certain plants (grasses, reeds, trees, etc.) growing so abundantly on a wide variety of soils, the answer to the problem of a wide distribution is readily provided, and their ubiquity in the soils is more logically explained.

The source of most of the phytoliths in any one soil assemblage may be quite local but this aspect has yet to be investigated in Victoria, by comparison of the phytoliths in the soils with those which undoubtedly occur in grasses, etc. growing on the site. Some phytoliths become wind-borne, as evidenced by studies of the mixed assemblages of phytoliths in "red rain" residues and in "red snow" residues. Others can be dispersed per medium of the dung of roaming herbivorous animals, and this factor may be of especial significance in Australia, in view of the widely and freely roving habits of the native herbivorous fauna in the not so distant past. Still others may be moved about as a consequence of sheet run-off of rainwaters, gathering into ephemeral bodies of fresh water, and later moved by wind transport on drying up of the waters, followed at times by precipitation in rain or snow or by normal settling. Some may have been moved from the original points of release from host plants as a result of gravitational soil creep or by erosion generally. Phytoliths removed from a source region, on being swept into watercourses, should ultimately reach the alluvial soils of river flood plains or even become incorporated in marine sediments, provided they are capable of withstanding transportation over long distances and other factors involved in sedimentary processes. Phytoliths still locked up in undecomposed grass leaves or wood, for example, would probably last longer and might be carried further by marine currents, particularly in driftwood, than phytoliths already freed from their plant hosts.

Phytoliths have not yet been specifically located in the roots of plants; they occur most commonly in leaves, more especially of grasses, and a few have been observed in the culms and flower-heads of grasses (Smithson 1958, pp. 153–4); they are also common in the wood of certain trees. The phytoliths in soils can occasionally be attributed to some particular grass, but more commonly they can only be assigned less definitely to a grass tribe, or even only to a group of grass tribes. It remains for botanical studies of Victorian phytolith-generating plants to show whether plant groups in any particular area provide a reflection of the variabilities encountered in particular soil assemblages. Once this is known, it may then be possible to determine whether winds or other agencies have played dominant roles in affecting the populations of phytoliths in soils, either by smoothing out the effects of a dominant local phytolith contribution or by introducing types from more distant sources. Detailed correlations of this nature would be closely associated with strengths and directions of winds, etc.

The facts that vast numbers of phytoliths occur in soils, and that some have evidently been subjected to certain degrees of corrosion in soils or to attrition in wind-borne dust, indicate that silica removed from the soil and precipitated as opaline silica in certain plants is ultimately returned to the soil, whether in the general area of development or in some far removed region. Soils are not choked with phytoliths, and this points to the establishment of a balance between the amount of phytoliths generated and shed into the soils and their subsequent fate in the sequence of events following upon initial release from the host plants.

A ton of gramineous matter per acre per year returns at least 2 per cent. of phytoliths. So it takes only 500 years to accumulate 10 tons per acre or 1 per cent. of the surface 6 inches. It seems likely therefore that there is a cycle of no more than 1000 years, and that in this time the previous phytoliths have restored their silica to the general circulation. This should not be surprising because there is always some silica in solution in soils, and opaline phytoliths should be among the first siliceous particles to dissolve.

The perpetuation of a population of opal phytoliths in soils depends upon the operation of many and varied processes that can become effective after their release from plant tissue. Among these are: (i) the rate of conversion from the hydrous opaline form to the anhydrous cryptocrystalline form of silica; (ii) processes resultant upon prevailing soil conditions at different sites and at different times; (iii) processes arising from extraneous agencies such as the effects of wind, water, animals, or grass fires.

In relation to (i), it is concluded that the opal phytoliths in Victorian soils provide evidence of having been released from the host plants relatively recently, and that the passage of time has been of too short duration, from the geological aspect, to result in conversion from opaline to cryptocrystalline silica (cf. Smithson 1956*a*, p. 125). In connexion with (ii), phytolith survival depends upon the variable pH range of soils, taken in conjunction with the relative age of a particular soil compared with that of its phytolith population. The weak acids or alkalies in the soils could probably only be effective in corroding and dissolving opaline silica if operative upon these minute bodies for a considerable period. Phytoliths newly released from their plant hosts would thus be little affected by these processes, but much older phytoliths may have been completely lost by solution. A few phytoliths of apparently intermediate age reveal some little evidence of corrosion.

During the short period of time necessary for the passage of phytoliths through the digestive tract of an herbivorous animal, or while incorporated as a constituent of animal dung, it is unlikely that the phytoliths would be significantly modified by animal acids. Among the effects of (iii), that of grass fires may be locally important; slowly smouldering grass-stacks and hay-ricks are known to leave a residue of natural silica glass about the size of a man's fist after the vegetable matter has been incinerated (Baker and Gaskin 1946, p. 100). It is therefore conceivable that grass fires, although transient, often local, and not of very great frequency, may nevertheless result in some modification of such minute opaline silica bodies as the phytoliths contained in grass leaves. Investigations to test this have not yet been conducted. Studies of phytoliths in wind-borne dust, precipitated with rain or snow, reveal that some have been fractured, probably during transportation. The resistance of phytoliths to other environments, such as water transportation, has not yet been assessed, but abrasion during sheet run-off of surface drainage waters would be expected to be only slight. The effects of attrition could, however, be more pronounced where phytoliths are washed into streams and swept along for considerable distances. This has yet to be determined from studies of various alluvial soils known to have been transported from remote sources.

Although studies of phytoliths in Victorian soils are only in the early stages, enough has been indicated herein to reveal that the history of these opaline bodies may be very varied in relation to space and time after their release from the host plants. Whatever the ultimate fate of any particular phytoliths, it becomes evident that their population in the soils is generally being maintained by a gradual, continuing shedding, by means of several processes, from phytolith-generating plants.

Since this paper was submitted, phytoliths have been reported from soils in Illinois by A. H. Beavers and I. Stephen (*Soil Sci.* **86**: 1 (1958)).

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The permanent mineral grain slides of the fine sand fractions of Victorian soils and of "red rain" residue, also the residue from "red snow", were kindly lent by the Geology Department, University of Melbourne. Mr. F. Chapman's original "red rain" residues were donated by the Royal Melbourne Technical College.

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A CONTRAST IN THE OPAL PHYTOLITH ASSEMBLAGES OF TWO VICTORIAN SOILS

By G. Baker*

[*Manuscript received August* 26, 1958]

Summary

A statistical analysis of the assemblages of opal phytoliths in two Victorian soils of different origin, occurring approximately 90 miles apart and supporting generally different plant communities, reveals that some shape types of the phytoliths are common to both soils, while significant differences occur in the amount and nature of other shape types. The general conclusion is that the phytoliths in soil from basaltic tuff on the summit of Mt. Gellibrand in the Western District derive from the local plant population; those in alluvial clay soil developed under swampy conditions at Dalmore, Koo-wee-rup Swamp, derive largely from the local swamp vegetation, with the possibility of the introduction of certain shape types from different plants supported on the southern Dandenong Ranges 18 miles to the north, and on intervening areas. Transportation into the swamp lands would have been effected by the watercourses flowing in from the north, once the phytoliths had been released from plants and shed into the soils near the watercourses. It is doubtful whether any significant proportion of the phytoliths was wind-borne into either of the soils examined.

I. Introduction

The opal phytolith content of an alluvial clay soil (Dalmore clay, normal type—see Goudie 1942, pp. 99–100, 104) accumulated under paludal conditions at Dalmore in the basin of Cardinia Creek, Koo-wee-rup Swamp, is compared and contrasted with that of a soil from basaltic tuff on the summit of Mt. Gellibrand, 5½ miles north of the Prince's Highway between Colac and Winchelsea, on the lava plains of the Western District (cf. Baker 1959).

These two localities are approximately 90 miles apart (in a direct line) and are situated respectively south-east and south-west of Melbourne. Dalmore is 2 miles from the coastline of Westernport Bay and is approximately 10 ft above sea-level. Mt. Gellibrand is 25 miles from the coastline of the Southern Ocean and is 871 ft above sea-level.

The fraction between 5 and 50 μ, which contains the greater proportion of phytoliths in soils, was obtained by decantation, distilled water and not tap-water always being used in order to avoid contamination. The size limits were estimated for particles with a specific gravity of 2·6. The fractions so obtained constituted 5 per cent. of the soil from Dalmore and 22 per cent. of the soil from the summit of Mt. Gellibrand. The topsoil (0–7 in.) was used in each sample.

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II. PERCENTAGE OF PHYTOLITHS IN THE 5–50 MICRON FRACTION

Counts of the constituents of the 5–50 μ fractions in clove oil (R.I. = *c.* 1·53) and Canada balsam (R.I. = *c.* 1·54) under a polarizing microscope revealed the proportions listed in Table 1.

The Mt. Gellibrand soil is among the richest in Victorian soils in its content of opaline silica bodies, but it is surpassed by the Dalmore soil. From the percentages of the 5–50 μ fraction in each soil and the respective counts of the different constituents shown in Table 1, it has been calculated that the phytolith populations amount to 2·6 per cent. of the Dalmore alluvial clay soil and 2·0 per cent. of the Mt. Gellibrand basaltic tuff soil. A further 0·6 per cent. of opaline silica occurs in the Dalmore and 0·1 per cent. in the Mt. Gellibrand assemblage in the form of diatoms and sponge spicules, or of diatoms alone. These percentage values are calculated on the broad assumption that the size and specific gravity of all the constituents present are much the same. Furthermore, the percentages have been derived by utilizing a weight percentage (for the quantity of the 5–50 μ fraction obtained) and a volume percentage (for the proportion by count of the phytolith population in the 5–50 μ fraction). Hence it is suspected that the percentage values estimated for the contents of phytoliths (see Table 1) may be too high. However, the lower specific gravity (*c.* 2·15) of the opaline bodies compared with that of quartz in the fractions is compensated to some extent by the fact that since these bodies were separated by decantation, they are somewhat larger than quartz particles which fall at the same rate.

TABLE 1

CONSTITUENTS OF THE 5–50 MICRON FRACTION OF TOPSOILS FROM DALMORE AND MT. GELLIBRAND

Particles	Dalmore (%)	Mt. Gellibrand (%)
Phytoliths	52·5	9·5
Diatoms	10·5	0·5
Sponge spicule fragments	0·2	0·0*
Mineral particles, etc.	36·8	90·0
Total	100·0	100·0
Number of particles counted	1017	1230

*Only one fragment of a sponge spicule observed in the whole of the preparation consisting of several thousand particles.

Table 1 also reveals the dominance of opal phytoliths over diatoms and sponge spicules in both assemblages.

III. Analysis of Phytolith Assemblages

The two phytolith assemblages have been analysed for shape distribution by counting methods; the various proportions of each shape type of phytolith in

Table 2

PERCENTAGE DISTRIBUTION (BY COUNT) OF PHYTOLITH SHAPE TYPES IN DALMORE AND MT. GELLIBRAND TOPSOILS

Outline Shape Resembling:	Illustrated in:	Dalmore (%)	Mt. Gellibrand (%)
Ball	—	1·3	0·8
Bean	Fig. 3, No. 87	tr.*	0·7
Berry	Fig. 4, No. 29	2·7	0·2
Boat	Fig. 2, Nos. 67, 68	0·8	5·1
Botryoidal	Fig. 3, No. 76	0·6	—
Capstan	Fig. 4, No. 25	0·7	0·8
Carrot	Fig. 4, No. 24	tr.	0·7
"Chunky"	Fig. 2, No. 59	1·1	4·0
Club	Fig. 4, No. 19	0·2	0·5
Dumbbell	Fig. 4, Nos. 39, 40, 43, 46	1·1	9·0
Dumbbell with double swelling	Fig. 4, Nos. 41, 42	0·2	1·2
Fan	Fig. 3, No. 97	0·6	0·3
Flask	Fig. 4, No. 23	0·2	0·3
Hat	Fig. 2, No. 66	0·5	2·1
Hatchet	Fig. 4, No. 4	0·2	0·2
Heart	Fig. 2, No. 39	0·2	0·7
Hourglass	Fig. 1, No. 17	0·3	0·3
Knucklebone	Fig. 2, No. 49	0·3	0·3
Nondescript and irregular	Fig. 1, No. 14 Fig. 2, No. 53	32·7	24·9
Oval	Fig. 3, No. 74	0·3	3·6
Pear	Fig. 2, No. 48 Fig. 4, No. 20	0·1	0·3
"Ragged" forms	Fig. 2, No. 33	1·1	0·5
Rods:			
Branched	Fig. 1, No. 11 Fig. 2, No. 50	0·5	0·3
Curved	Fig. 1, No. 6	0·5	0·8
Hooked	Fig. 1, No. 18	0·3	0·2
Saw-edged	Fig. 1, No. 9	0·5	0·7
Smooth-edged	Fig. 1, No. 5	32·6	25·7
Spinose	Fig. 1, No. 19	1·3	0·7
Tapered	Fig. 4, No. 16	0·6	0·8
Wavy-edged	Fig. 1, No. 1 Fig. 4, No. 1	1·9	9·0
With opaque cores	Fig. 1, No. 3	0·3	1·4
Roman lamp	Fig. 3, No. 77	0·2	—
Spearhead	Fig. 1, No. 4	0·5	0·6

* tr., Trace.

TABLE 2 (*Continued*)

Outline Shape Resembling:	Illustrated in:	Dalmore (%)	Mt. Gellibrand (%)
Spindle	Fig. 4, No. 31	0·1	0·7
Star	Fig. 2, No. 65	4·9	—
Tooth	Fig. 1, No. 22 Fig. 4, No. 33	0·6	1·0
Wedge	Fig. 4, No. 36	0·9	0·3
Worm	Fig. 3, Nos. 93, 94	3·3	—
Cuticle replacements	Fig. 3, Nos. 79, 86	4·1	0·3
Hollow casts of cell walls (= cell linings)	Fig. 3, No. 92	0·8	0·3
Rectangular plates (often ridged)	Fig. 4, No. 18	0·9	0·7
Total		100·0	100·0
Number of phytoliths counted		635	587

each assemblage are shown in Table 2. The shape terms employed are largely taken from resemblances of the outlines of the opal phytoliths to those of commonplace objects. A considerable proportion in each assemblage is constituted of nondescript shapes.

Table 2 reveals that both assemblages are dominated by two groups of phytoliths: rod-shaped forms and nondescript types. Together these constitute 71 per cent. of the Dalmore assemblage and 65 per cent. of the Mt. Gellibrand assemblage.

The total percentages of all varieties of rod-like phytoliths are comparable for the two soils—38·5 per cent. of the Dalmore population and 39·6 per cent. of the Mt. Gellibrand population—but detailed analyses of the varieties of the rods reveal some significant differences. Thus rods with smooth edges are more common in the Dalmore assemblage, rods with wavy (crenulated and embayed) edges are much less common, while notably fewer rods with opaque cores are represented. The other types of rods, however, show little difference in the amounts present, although spinose rods are rather more frequent in the Dalmore assemblage.

There are approximately 9½ per cent. fewer dumbbell- and bean-shaped phytoliths, and 6 per cent. fewer hat- and boat-shaped forms, in the Dalmore assemblage. These lower values are compensated by: (i) increased quantities of ball- and berry-shaped phytoliths (3 per cent. more); (ii) the presence of types not represented in the Mt. Gellibrand assemblage, e.g. botryoidal, star-like, and the minute worm-shaped forms, which together amount to approximately 9 per cent.; (iii) increases of just over 4 per cent. of such types as the cuticle replacements and the hollow casts of cell walls (cell linings).

Nondescript and irregular types of phytoliths (including "ragged" forms) are approximately 8½ per cent. in excess in the Dalmore compared with the Mt. Gellibrand assemblage, but heart-, spindle-, and oval-shaped, and "chunky" types constitute a compensating excess in the Mt. Gellibrand assemblage.

IV. Phytolith Shapes and Sizes

The typical and the less common phytoliths listed in Table 2 are illustrated to scale in Figure 1 (Nos. 1–32), Figure 2 (Nos. 33–71), and Figure 3 (Nos. 72–106) for the Dalmore assemblage, and in Figure 4 (Nos. 1–52) for the Mt. Gellibrand assemblage.

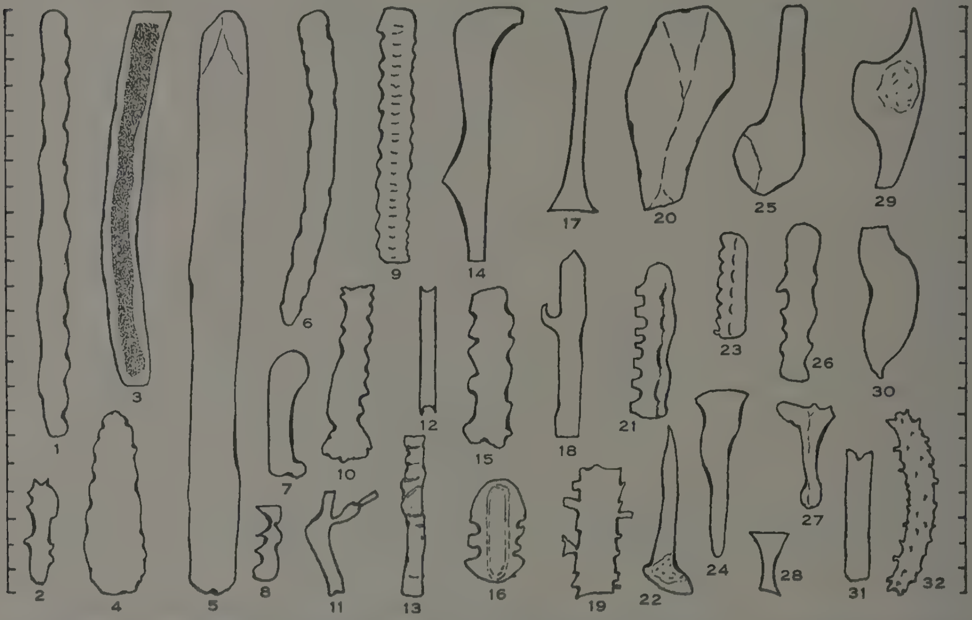

Fig. 1, Nos. 1–32.—Opal phytoliths from Dalmore alluvial clay soil, Koo-wee-rup Swamp. Each scale graduation represents 0·010 mm.

The diagrams mainly represent outline sketches only of phytoliths as they appeared in positions of rest in the mounting media; they were sketched at a magnification of ×360 under a petrological microscope, and each form was checked for isotropism. A few sculptural elements have been added to some of the sketches.

(*a*) *Dalmore Phytolith Assemblage*

Mounts of the 5–50 μ fraction of the Dalmore topsoil reveal a most striking and abundant array of opal phytoliths, many of which are water-clear and colourless.

Some of the rod-like forms are thicker than others; examples 0·15 mm long are 0·04 mm thick, but the more common thinner rods range from 0·010 to 0·125 mm in length and from 0·005 to 0·007 mm in thickness. All such types have relatively smooth outlines. The largest rod observed is smooth-edged and measures

0·40 mm long and 0·02 mm thick; the largest wavy-edged rod measures 0·275 mm long and 0·025 mm thick. Some rods are "prickly", others denticulate along one or sometimes both of the longer edges. Other rods are crenulate or sometimes irregularly embayed by corrosion. One rod revealed a curved, hook-like process as shown in Figure 1, No. 18.

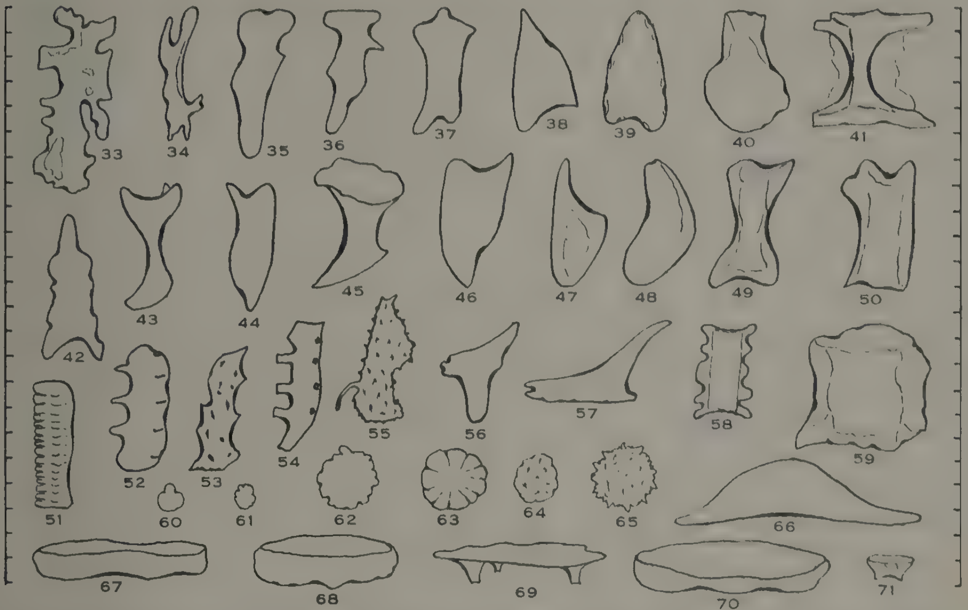
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Fig. 2, Nos. 33-71.—Opal phytoliths from Dalmore alluvial clay soil, Koo-wee-rup Swamp. Each scale graduation represents 0·010 mm.

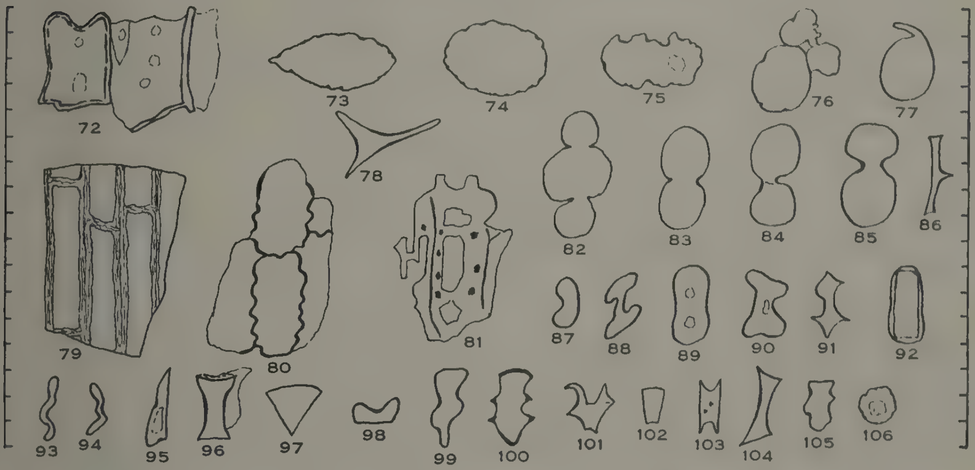
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Fig. 3, Nos. 72-106.—Opal phytoliths from Dalmore alluvial clay soil, Koo-wee-rup Swamp. Each scale graduation represents 0·010 mm.

Berry-like forms are sometimes smooth, occasionally rugose, and more rarely spinose; they range from 0·005 to 0·035 mm in diameter and average 0·015 mm. "Chunky" forms range from 0·050 to 0·005 mm in size. Worm-shaped examples (Fig. 3, Nos. 93, 94) are generally 0·025 mm long, 0·004 mm thick, and always devoid of ornamentation.

"Ragged" phytoliths such as that shown in Figure 2, No. 33, are known to occur within the cells of some woods. As they are observed in this soil, they consist of water-clear opal (var. hyalite) and are always free from included matter.

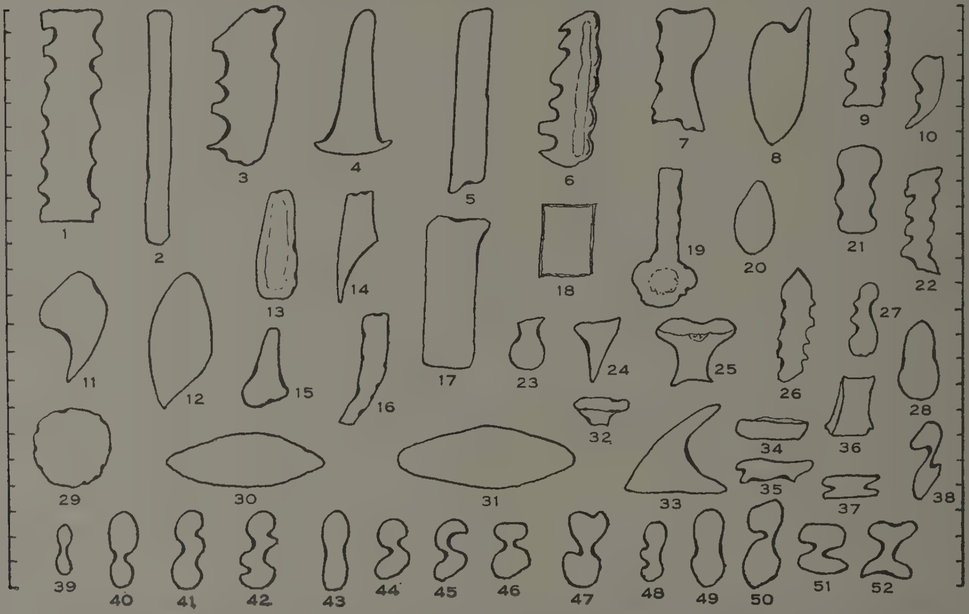

Fig. 4, Nos. 1–52.—Opal phytoliths from Mt. Gellibrand basaltic tuff soil, Western District. Each scale graduation represents 0·010 mm.

A few oval-shaped phytoliths (Fig. 3, No. 75) have evidently been corroded after release from the plant host.

One piece of plant tissue in a mount of the 5–50 μ fraction revealed seven small, rod-like phytoliths *in situ*. Some of these are smooth, one or two are ornamented with minute knob-like protuberances and low ridges, and their average size is 0·030 mm long and 0·007 mm thick.

Examples of phytoliths representing cuticle replacements reveal simple and complex casts of cell wall structures (Fig. 3, Nos. 79–81). Those with crenulate outlines (Fig. 3, No. 80) are typical of the outer epidermis of grasses, and it is apparent from such examples that the rod-like phytoliths with wavy edges (e.g. Fig. 4, No. 1) represent solid infillings (internal casts) of these types of cells.

The general characteristics of other varieties of the phytoliths are depicted in Figures 1–3.

(*b*) *Mt. Gellibrand Phytolith Assemblage*

Whereas the 5–50 μ fraction of the Dalmore topsoil is light grey in colour, that of the Mt. Gellibrand fraction is reddish brown. Although this colour difference is principally due to different proportions of organic matter or iron compounds or both in the two fractions, colour variations among the phytoliths themselves partly contribute to the overall colour difference. Thus the greater proportion of the Dalmore phytoliths are clear and colourless or merely have a light pinkish brown cast, while many of the Mt. Gellibrand phytoliths are more distinctly brownish in colour.

Rod-like phytoliths dominate the assemblage, and are followed in abundance (apart from the total nondescript forms) by dumbbell-, boat-, and oval-shaped, and "chunky" forms. The rods are generally not as slender as those in the Dalmore assemblage. The largest rod observed measures 0·20 mm long and 0·015 mm thick. Although fewer in number, ball- and berry-shaped phytoliths are approximately twice as large as the Dalmore examples. Some of the minor variations in size and shape in the group of the dumbbell-shaped phytoliths are shown in Figure 4, Nos. 38–52. None of the dumbbell nor allied types exceeds 0·035 mm in length: the shortest measures 0·020 mm and the average length is between 0·025 and 0·030 mm.

V. PRINCIPAL DIFFERENCES AND SIGNIFICANCE OF VARIATIONS IN THE OPAL PHYTOLITH ASSEMBLAGES

The principal differences between the two assemblages are brought out by the following items: (i) the somewhat greater overall content of phytoliths in the Dalmore topsoil; (ii) its greater array of shape types, more especially among nondescript forms; (iii) its greater abundance of such types as ball-shaped, berry-shaped, "ragged", star-shaped, and worm-shaped forms; (iv) its more abundant cuticle replacements. The Mt. Gellibrand topsoil reveals: (v) a greater abundance of bean-, boat-, dumbbell-, heart-, hat-, oval-, and tooth-shaped, and "chunky" forms; (vi) among the rod-like types, wavy-edged rods are approximately five times as abundant, spinose rods half as abundant, and smooth-edged rods markedly less common than in the Dalmore topsoil; (vii) fractured phytoliths are rather less plentiful than in the Dalmore assemblage.

The significance of the variations in the two phytolith populations lies fundamentally in the peculiarity of certain plants in secreting opaline silica in certain of their structural elements; and partly in the fact that one assemblage (Dalmore) occurs in an alluvial clay soil from a reclaimed swampy area, while the other assemblage (Mt. Gellibrand) occurs in a hilltop soil from a volcanic (basalt tuff) area. The supply of opal phytoliths to each soil has evidently followed a rather different pattern in the two areas. Certain similarities between some of the components of the two phytolith populations suggest an origin from similar types of phytolith-generating plants in the separated areas. These components entered the soil more or less *in situ* on decomposition or destruction of the local phytolith-bearing vegetation. The striking variations in the nature and quantity of other types of phytoliths in the two assemblages point to an origin from different types of plants, or else to development in certain structural elements of the same plant families in one area and not in the other. Moreover, they may have been shed from plants growing either in the area concerned or in more remote areas, or both; this applies more especially to the Dalmore assemblage.

Dalmore is approximately 2 miles west of south of the junction of Cardinia Creek and Toomuc Creek. These two watercourses and their tributaries drain the timbered granodiorite hills lying 18 miles to the north, and they arise in the Aura–Clematis–Emerald–Cockatoo districts, near the dacite–granodiorite contact of the southern Dandenong Ranges. Opal phytoliths in the alluvial clay soil at Dalmore could therefore be derived partly from the vegetation (trees and undergrowth) supported on these hills, and partly from vegetation (grasses etc.) growing on the Silurian regions forming the southern flanks of the granodiorite hills. The main source, however, is considered to be the phytolith-bearing plant community (tea-tree, reeds, rushes, and introduced pasture plants) of the reclaimed swamp region around Dalmore, where the reed *Phragmites communis*, for example, is of common occurrence.

The principal source of opal phytoliths in the Mt. Gellibrand topsoil evidently lies in the local phytolith-bearing vegetation covering the summit of the mountain, both prior and subsequent to utilization of the area for farming.

In neither region can wind transportation be proved responsible for contributing significant quantities of phytoliths from outside sources.

The facts that: (*a*) the Dalmore soil, which is only 10 ft above sea-level and 2 miles north of Westernport Bay, contains more sponge spicules (see Table 1) than the Mt. Gellibrand soil, which is 871 ft above sea-level and 25 miles from the Southern Ocean, and (*b*) the sponge spicule content of each soil forms a very minor portion of the 5–50 μ fraction—together point to the probability that recent marine sponge spicules, at least, do not become widely dispersed in important amounts by wind from sea-shores to inland areas. The introduction of greater quantities of sponge spicules into the Dalmore soil could well be influenced by the fact that the watercourses entering the sea nearby are tidal for 2 miles or more from their mouths.

VI. ACKNOWLEDGMENTS

The author is indebted to Associate Professor G. W. Leeper, University of Melbourne, for kindly supplying samples of the 5–50 μ fractions of the Dalmore and Mt. Gellibrand topsoils, and for criticism of the manuscript.

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CONTROL OF WATER MOVEMENT BY STEM CHILLING

By R. D. Johnston*

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Summary

Apparatus is described whereby a portion of the stem of a young tree of *Pinus radiata* D. Don could be maintained at a temperature close to freezing point, while the transpiration of the upper part of the plant was measured. The freezing point of the stem was shown to be about −2·0°C, and while the stem temperature was kept above this point transpiration continued normally; freezing the stem resulted in a decrease in transpiration, after a short lag period, and within 3 hr transpiration was almost undetectable.

When the stem temperature was maintained at just below the freezing point for 7 days, the leaf water deficit of the shoot rose from 10 to 47 per cent., but returned to normal values within 4 days after freezing was stopped; the plant showed no signs of damage due to freezing.

Field trials, using solid carbon dioxide as a refrigerant, showed that growth was reduced considerably on a branch chilled to −4°C for 7 days, but needles remained alive and appeared healthy. Lower temperatures caused damage to needles and twigs.

I. Introduction

The investigation of the effects of drought on plants is hampered by certain difficulties which result from the interaction of the factors involved. One of the difficulties is that when watering of the soil is stopped in order to limit the supply to the plant, there are effects on the roots as well as the tops. Root growth ceases and roots become suberized to the tip (Kramer 1949) and may die. When watering is resumed, the roots take up water and recommence growth. The rate of uptake is not necessarily the same as it was before droughting, however; Kramer (1950) showed that for tomato plants which were wilted and rewatered, the original transpiration rate was not approached for 3–4 days after rewatering, and sunflower plants showed very little recovery in the same time.

One method used in attempting to separate the effects of drought on the shoot from those on the root has been to work on severed plant parts. These parts may be leaves (Pisek and Berger 1938) or branches (Parker 1954). But with severed parts a second difficulty arises, namely, the separation of drought effects from the effects of cutting. Cut stems may become plugged with resin (Parker 1956) or latex (Kramer 1949) and even when this does not occur, cut branches do not live indefinitely. In order to assess recovery from near-lethal drying, tests of relatively short duration have been devised. These tests have been reviewed by Parker (1956); they include the use of tetrazolium salts, respiration measurement, and microscopic examination of sections, and are based on evidence of normal appearance, function, or reaction of the tissue a short time after treatment. They do not indicate whether the plant as a whole is able to resume its normal pattern of growth.

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If it is required to produce drought conditions in the shoot alone, without interfering with the roots, the water supply through the stem might be restricted artificially; but this restriction should be removable and no mechanical or physiological damage should be done to the plant directly by the restriction.

The use of low temperatures seems to be one means of fulfilling these requirements. Handley (1939) chilled the stems of sycamore and ash plants to temperatures of about 0°C and produced wilting, which indicated a reduction in water movement. The wilted plants recovered when the (stem) temperature was raised to +2°C. Handley also quotes the work of Kosaroff (1897), who produced wilting in the leaves of several species by cooling lengths of their stems to 0 to −2°C, but found that other species could be cooled to −4 to −5°C without wilting.

Went and Hull (1949) found that chilling a short length of the stem of tomato reduced the translocation of carbohydrates, but at +3°C had no appreciable effect on water movement. Similarly, Swanson and Whitney (1953) claimed that localized low temperatures retarded downward movement of radioactive substances in bean stems but not upward movement from the roots; their figures indicate, however, that all movement ceased at +5°C.

Kramer (1942) cooled the soil in which plants of various species were growing and found that uptake of water was reduced, the critical temperatures differing considerably between species, while Kozlowski (1943) showed a species difference between loblolly and white pines, in the rates of loss of water from potted plants at different soil temperatures. For both species there was a sudden decrease in the rate of loss, between +5 and +1°C.

The great decrease in water uptake by many of the species when temperatures were reduced but still above 0°C, and Handley's report of reduction in water movement by stem chilling without freezing, indicate that it may be possible to control water movement by chilling a length of the stem without freezing, or at least without causing damage due to freezing. Accordingly, during research work at the Imperial College of Science and Technology, London, apparatus was constructed and investigations made to determine:

1. The freezing point of the stem of a small, potted plant of *Pinus radiata* D. Don.
2. The relationship between transpiration and stem temperature, near to the freezing point.
3. The possibility of reversibly increasing the leaf water deficit (L.W.D.) by keeping part of the stem at a controlled low temperature.

II. APPARATUS

(*a*) *To Chill Plant Stem*

The basic element in the apparatus for chilling the stem of the plant was a converted household refrigerator motor and compressor. "Freon" was used as the primary coolant, which was circulated through a $\frac{3}{8}$ in. copper pipe lining a 12 gal reservoir. The reservoir was filled with a secondary coolant, a mixture of ethylene glycol and water, which could be maintained at any temperature from ambient to −10°C (±1°).

Coolant from the reservoir was withdrawn by a small (Stuart Turner No. 10) electrically driven centrifugal pump, normally running continuously. Most of the liquid was returned directly to the reservoir through a circulation pipe, which was provided with a throttle to regulate the flow rate and to produce the back pressure necessary for efficient operation of the pump.

The flow of coolant to the plant consisted of two parts: a by-pass, controlled by a throttle, allowed a small continuous flow to balance the heat gains along the lines and so prevent an upward surge of temperature when the valve was opened; while the direct line, which was provided with a solenoid-operated valve, allowed periodic increases in the flow rate, to maintain the temperature in the jacket at the desired level.

This jacket, which surrounded an 8 in. long portion of the plant stem, was formed of several parallel sections of thin-walled rubber tubing (cycle inner tubing) stoppered at each end and connected by short pieces of glass tubing to the rubber tubes through which the coolant was pumped. The whole of the apparatus was well insulated with cotton wool and metal foil.

The solenoid-operated valve was controlled through a relay by a mercury-in-glass thermoregulator, which was enclosed with the portion of the stem in the cooling jacket. This thermoregulator had a temperature differential of about 0·2°C, and under operating conditions the stem temperature could be controlled to within 0·5°C.

Temperature of the stem was measured by a copper-constantan thermojunction inserted through the bark and about 1 mm into the wood, at about the mid point of the part of the stem covered by the jacket. The thermocouple leads were covered with plastic tubing within the jacket and were connected to a cold junction, immersed in melting ice in a thermos flask, and a Doran "Mini" thermocouple potentiometer.

(*b*) *To Measure Transpiration*

The method adopted for the measurement of transpiration during chilling experiments is based on the measurement of changes in humidity of the air during its passage over a sample branch of the plant. A relative humidity recorder was used in this way by Thomas and Hill (1937) and the use of a corona discharge tube and counter as a recording hygrometer for transpiration measurement has been described by Andersson, Hertz, and Rufelt (1954). Huber and Miller (1954) used the rise in temperature associated with solution of water vapour in sulphuric acid to estimate the humidity of the air stream, and Decker (1956) measured changes in humidity with a modified CO_2 analyser. Preston (1954) suggested the use of wet and dry thermocouples in the way they have been used here, although no details of actual application were given.

There are some disadvantages in the use of humidity measurements to estimate transpiration: the plant or part of it must be enclosed in order that the volume of air absorbing the transpired water can be measured, and the flow rate must be sufficiently high so that the air does not become saturated at any time. Enclosing the plant alters the disposal of its leaves as well as reducing, through absorption and reflection by the envelope, the amount of light falling on the leaves.

The consequent reduction in transpiration may be considerable; in a test with small plants the water loss of a test plant compared with that of a control plant was reduced by about 20 per cent. by covering and drawing air through the cover. Where both treated and control plants are covered, however, much of the difference may be eliminated, and by comparing the ratios of transpiration of the two plants before and during treatment a comparative measure of the effect of treatment may be made.

The primary advantage of using this method is that where weighing of the whole plant is impracticable large plants may be sampled without damage. The size of the sample is limited by the rate of air flow attainable, since, depending upon temperature and humidity of the incoming air, up to 1 litre/min/g fresh weight may be required to remove the transpired water from conifers. A second advantage is that transpiration from the same sample may be measured repeatedly, and by using recording instruments continuous records can be made.

The apparatus used consisted of a polyethylene sleeve which was placed over the sample branch, with transparent PVC air intake and exit tubes. The intake orifices of tubes for each air line were grouped to take in air from the same point.

Air passing from the sleeves and through the exit line moved past the dry and wet bulb temperature-sensing elements of the humidity units, through flowmeters graduated to 0·1 l./min and into the suction reservoir of a small diaphragm pump. Each humidity unit consisted of a short length of PVC tubing into which projected two copper-constantan thermojunctions. The leading one of these, i.e. the one nearer to the plant, was bare and measured the dry bulb temperature of the air. The trailing unit was covered by a cotton wick which passed through a hole in the under-side of the PVC tubing into a small reservoir of distilled water.

The cold junctions of all thermocouples were fastened around the edge of a small circular cork separator and kept immersed in a mixture of distilled water and ice, in a thermos flask.

Potentials of the thermocouples were measured by a Doran "Mini" thermocouple potentiometer.

Air was drawn through the apparatus at a constant rate, maintained by throttles on the suction lines and a controllable leak to the suction reservoir. The potentials of the three pairs of thermocouples were measured in turn; if readings showed any fluctuations, a second set in reverse order was taken and the means of the two used. These potentials were converted into temperatures and the combinations of wet and dry bulb temperatures converted to air humidity in milligrams per litre.

Then the difference between the humidities of plant and air lines, multiplied by the flow rate, represents transpiration.

III. RESULTS

(a) *Freezing Point of Stem*

The chilling apparatus was operated to reduce the stem temperature at a measurable rate, the coolant being maintained at a temperature of −10°C. Stem temperatures were measured at 1 min intervals. The results, illustrated in Figure 1, showed first a rapid fall in temperature, then a sharp rise, followed by oscillations of decreasing amplitude and finally a further fall. The significance of these fluctuations, and the interpretation of temperature data, will be discussed later. The mean temperature at freezing point was concluded to be —1·9°C.

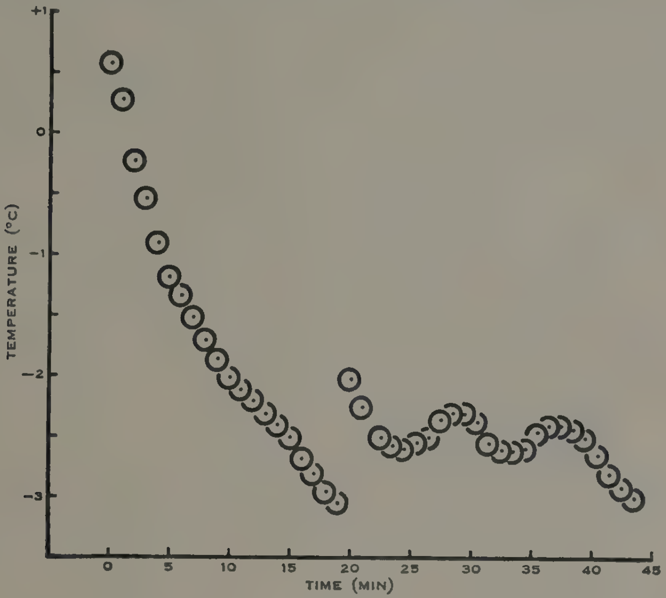

Fig. 1.—Determination of freezing point of stem. An 8 in. length of stem was surrounded by a jacket through which chilled liquid was pumped. Temperatures were measured by a thermocouple inserted about 1 mm into the wood, in the middle of the chilled zone.

(*b*) *Effect of Stem Temperature on Transpiration*

(i) *Control Run at Normal Air Temperatures.*—Two similar plants of 3-year-old *P. radiata* growing in moist soil in pots were used for transpiration measurements. A sample branch of about the same size on each, with an estimated 10 g fresh weight of needles, of 2 years' growth, was enclosed in the polyethylene sleeve and air drawn over it at 5 l./min. The calculated transpiration from each in milligrams of water per minute is shown in Figure 2(*a*).

Changes in transpiration followed rather closely the changes in light intensity due to movements of clouds and of the shadows cast by structural beams in the conservatory where the work was performed.

The relative values of transpiration for the two branches changed during the day, that of the control plant being slightly lower in the early part of the morning but higher through most of the day. This appears to be a position effect associated with slight differences in attitude of the branches, coupled with the effect of a small difference in sample size.

(ii) *Temperatures below Freezing Point.*—The temperature of the stem of the treated plant was reduced to between $-2\cdot0$ and $-2\cdot5$°C and transpiration measured as for the normal temperatures. Results are shown in Figure 3(*a*). Cooling of the stem was commenced at 10 a.m., when the transpiration rates of both plants were rising steeply. The temperature of the treated part of the stem fell to -2°C by 10.30 a.m., but no effect was noted on the transpiration rate until after 11 a.m. when a sharp decrease occurred. This lag is interpreted as corresponding to the time needed for reduction of water content of the plant tissues above the zone of freezing, to a level at which stomatal control of transpiration became effective. Between 11.45 a.m. and 12.45 p.m., fluctuations in the transpiration of the treated plant tended to follow those of the control, but at about half the absolute rate. By 1.15 p.m., that is, about 3 hr after the stem chilling had been applied, the transpiration of the treated plant had practically ceased. Cooling was maintained overnight, and the following day transpiration was slight but measurable (Fig. 3(*b*)).

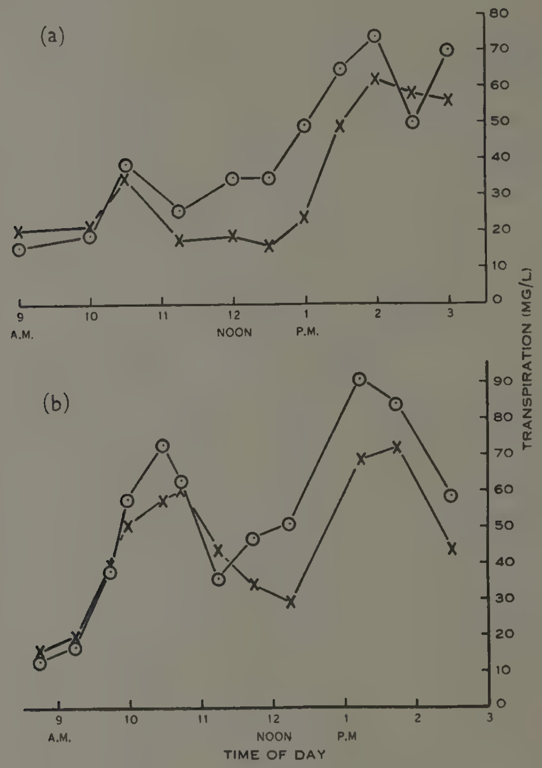

Fig. 2.—Comparative transpiration rates. (*a*) Both plants at ambient temperature. (*b*) Treated plant at $-1\cdot2$ to $-1\cdot7$°C.

(iii) *Temperatures between 0°C and Stem Freezing Point.*—In order to see whether chilling the stem without actually freezing it would cause reduction in transpiration, the stem temperature was reduced to the range −1·2 to −1·7°C, and transpiration measured as before.

Results are shown in Figure 2(*b*). The relative rates of transpiration are similar to those at normal temperatures.

(*c*) *Effect of Low Stem Temperatures on Leaf Water Deficit*

(i) *Potted Plants in Glass-house.*—It has been shown that transpiration may be greatly reduced by chilling part of the stem to just below the freezing point. While some slight transpiration continues it appears possible to allow the L.W.D. to increase to any desired level by this method. One question is whether the deficit will return to normal when chilling treatment is stopped. An experiment was therefore conducted to determine the effect on L.W.D. of maintenance of a part of the stem at between −2 and −3°C, for a period of several days, followed by return to normal temperatures.

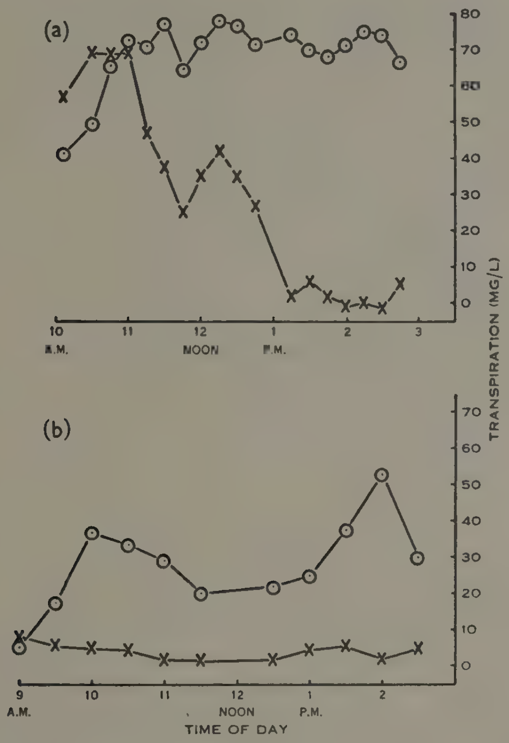

Fig. 3.—Comparative transpiration rates. (*a*) Treated plant at −2·0 to −2·5°C. (*b*) Treated plant maintained overnight at −2·0 to −2·5°C.

Chilling treatment was commenced on July 12 and ended on July 19; during this period the weather was mostly fine and sunny, and evaporation rates were high. No measurement of transpiration from the treated plant was made, but duplicate samples, for the determination of L.W.D. of both current year's needles and 1-year-old needles, were taken at 9 a.m. each day.

Results are shown in Figure 4. The L.W.D. increased very rapidly during the first day of treatment and continued to increase at a slightly slower but still considerable rate for the rest of the treatment period. Slight wilting of the youngest needles was evident after the fourth day.

When the chilling treatment was stopped the L.W.D. decreased rapidly for 2 days, then more slowly. It had not quite reached the original level 4 days after the normal stem temperature had been restored; the amount of water taken up during this period was 35 per cent. of the water content at saturation, which is approximately equivalent to the amount transpired in 1 hr under conditions of high transpiration.

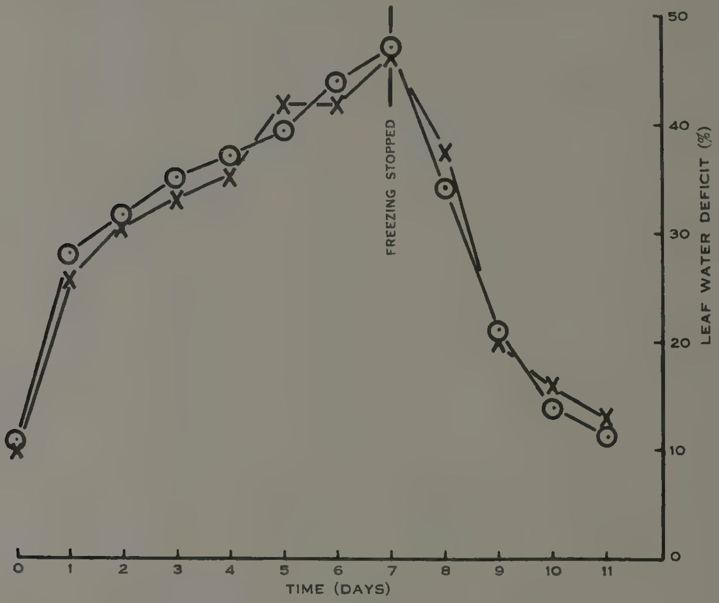

Fig. 4.—Effect of stem freezing on leaf water deficit. ⊙ New needles. × Old needles.

The plant subjected to the above treatment was examined about 1 month after treatment ceased, having been watered regularly meanwhile. Many of the 3-year-old needles had become discoloured, showing various colours from yellow to red-brown, and were easily dislodged. Otherwise the plant appeared normal. From observations of other plants which had been subjected to drought in the usual manner, the premature death of older needles is interpreted as an effect of drying rather than freezing; no signs could be observed which could not be the effects of high water stress and it was concluded that the relatively mild chilling treatment had not caused any direct damage.

(ii) *Field Application of Chilling Treatment*.—The successful production of high L.W.D. values in potted plants under glass-house conditions indicated that this method might be useful for the production of drought conditions in the field, independently of soil moisture availability. Accordingly, treatment was applied to restrict the water supply to a branch of a *P. radiata* tree growing in Windsor Great Park.

The need for portability and the lack of a power supply dictated the choice of solid carbon dioxide, "Cardice", as a primary coolant for field use. Since the sublimation temperature of carbon dioxide is —75°C, it was far too cold for direct application, however, and a conducting system was used to reduce the heat flow rate.

The "Cardice" was housed in a double-walled carton, well insulated with paper, cotton wool, and metal foil, and covered with a sheath of polyethylene film to protect it against the weather. The box was closed at the top by a double insulated lid. Within this carton the "Cardice" block stood on an aluminium plate which in turn rested on several strands of heavy copper wire. This wire was continued through the side of the box for a distance of about 40 cm, ending in a series of loops, which could be wrapped around the branch. When in position with a mercury thermometer inserted between the wire and branch, this conducting system was wrapped with insulation. By trial and error, a sufficient length of wire and sufficient tightness of wrapping were obtained to give approximately the required temperature range.

Three separate branches were treated:

(1) In the first, temperature was maintained at about —4°C for 1 week, being checked each morning when samples of 1-year-old needles were taken for the determination of L.W.D. In spite of cool weather, the L.W.D. rose from 15·3 to 24·0 per cent. in 24 hr, after which it continued to rise much more slowly, to 38·0 per cent. after 1 week's treatment. The deficit of a control branch at this time was 11·5 per cent. Treatment was stopped and the L.W.D. of the treated branch had returned to 14·5 per cent. after 3 days.

Growth of the shoots and new needles was markedly checked by this treatment and they did not grow to the same length as those of the control branch; the growth of the shoot (in length) and the number of needles in the following year were also reduced, although needle length was normal. See Plate 1.

(2) The temperature of the second branch was reduced to about —6°C and maintained at this temperature for 10 days. L.W.D. of 1-year-old needles rose from 11·0 to 28·8 per cent. in the first 24 hr and was 38·3 per cent. at the end of the period. At this stage the 3-year-old needles were becoming discoloured and the 1- and 2-year-old needles appeared normal, but the new needles were wilted and many had become brown at the base. Stem tissues of the new growth on a few branchlets were showing signs of shrinkage. At this point chilling was stopped; in the following 48 hr the L.W.D. fell to 17·9 per cent., with a further fall to 11·8 per cent. in the next 24 hr.

In spite of the decrease in deficit of the 1-year-old needles, many of the older needles turned brown and fell off. The new needles which had wilted and collapsed at the base also failed to recover and many of the new shoots died later. Growth of surviving shoots was markedly restricted in the following year. See Plate 2.

(3) Treatment of the third branch was more severe, the temperature falling to —10°C, and being maintained below —5°C for a period of 24 days. The weather

during this period was continuously dull, cold, and rainy, but the L.W.D. rose from 11·2 to 24·7 per cent. in the first 24 hr and continued to rise slowly to a maximum of 35·8 per cent. On removal of the treatment it fell to 19·1 per cent. in the first 24 hr and to 11·0 per cent. in the next 24 hr.

The 3-year-old and some of the 2-year-old needles on this branch became brown during the treatment period, and fell off. The new needles wilted during the first 24 hr and towards the end of the period the stems of new growth on a few branchlets were shrunken and discoloured; these shoots failed to recover.

The branch appeared for a while to recover on cessation of the chilling treatment but subsequently died.

IV. DISCUSSION

The work reported above has an immediate practical value in showing the relationship of water conduction to temperature near the freezing point, enabling an assessment to be made of the possibility of controlling L.W.D. without damaging the plant. In addition, the results of the work have more fundamental significance in the problem of the importance of vital factors in the transport of water through plant stems. In this respect the point of major interest is whether transpiration is actually reduced before the stem freezes, and the determination of the freezing point is important from this aspect.

In the determination of freezing point the graph of temperature against time in Figure 1 shows an initial fall, a sharp rise, then oscillations of decreasing amplitude before a final fall. This curve differs from the normal shape of the temperature/time curve during the freezing of liquids in cryoscopic determinations, since in the latter the rise as freezing commences is followed by a period when the temperature remains almost constant during freezing. Luyet and Gehenio (1937) found a double freezing point for living plant tissues and suggested that the first represented freezing of liquid in intercellular spaces. The series of apparent freezing points found here might equally well be an effect of the freezing of successive layers of tissue, resulting from low heat conductivity and the impossibility of stirring. The decrease in maximum temperature at each oscillation could result from the fact that the tissue which is in process of freezing is becoming further from the thermojunction, which would register the temperature of the outer layer of wood. On this interpretation the maximum temperature of the initial rise appears to be the best estimate of the freezing point.

In the measurement of transpiration, the difference in transpiration between the two plants was slight under normal temperature conditions and the same pattern of differences was shown when the temperature of the treated stem was maintained at 0·7–0·2°C above the determined freezing point. Reduction of the stem temperature to 0·1–0·6°C below the freezing point caused a reduction in transpiration, over a period of less than 3 hr, from 70 mg/min to almost nothing, while the control continued to transpire at about the same rate. This suggests that the cause of reduction in water movement is a physical one, due to freezing, and that in *P. radiata* the effect of stem temperature on water conduction is very slight while the stem is unfrozen.

Handley (1939) suggests, on the other hand, that for ash and sycamore the water conductivity of the stem is markedly reduced at temperatures between 2 and 0°C, although the freezing point of the sap in the stem is quoted from Dixon (1914) as —11°C and from Ewart (1908) as —7°C. The results of the work reported here give no evidence to confirm Handley's findings. A few points, however, deserve comment. Handley, using liquid circulating in thin-walled lead piping to chill the entire stem, measured the temperature of the air space between the tubing and the stem. No mention is made of temperature gradients along the stem, although these evidently existed, and no direct measurement of freezing point was made. Dixon's figures (Dixon and Joly 1895), quoted by Handley, were for *Taxus baccata* and appear to be exceptionally low, since most freezing points of plant tissue are above —5°C (Meyer and Anderson 1939).

It appears to be quite possible that the freezing points of the stems used by Handley were much closer to 0°C than was assumed by him and that the temperature did in fact fall to the freezing point at some part of the stem.

Under the circumstances the unqualified quotation of Handley's results as evidence of a vital force in the movement of water through the stem appears to be unjustified.

In view, however, of the large differences between species in ability to absorb water from soils at low temperatures (Kramer 1942), it is probable that similar differences exist in the relationship between the water conductivity of the stem and the temperature. This appears to be a matter for further investigation.

When water movement through the stem is prevented by freezing part of the stem, the only replacement of water lost from the needles in transpiration will be by a decrease of water content of the upper stem. The amount made available in this way is very small, compared with the amount which would be removed from the soil during drying. Therefore, when transpiration rates are high, L.W.D. rises rapidly. Under glass-house conditions, a slightly lower rate of water loss was maintained after the first 24 hr but, in the field in cloudy weather, the rise in L.W.D. above about 25 per cent. was extremely slow, which suggested that water loss was also very slow and that stomates remained closed under these conditions.

The maximum L.W.D. attained by the three branches which were treated in the field was approximately the same, about 38 per cent., although the treatment was applied for different periods. This was a result of steadily deteriorating weather conditions. The maximum deficits reached were considerably below those at which damage appeared in plants in the glass-house. The damage suffered, however, appears to be a function of the severity of chilling rather than the degree of water stress, temperatures below —5°C causing severe damage.

On the other hand, it appears possible to maintain temperatures between 0 and —5°C for periods of at least a week without killing any part of the plant. High deficits can be induced by this method, and the growth of shoots and needles is affected in a manner similar to that usually attributed to drought. The technique of controlling water movement, and of inducing drought stress, by stem chilling under closely controlled temperature conditions seems to be a very useful one.

V. ACKNOWLEDGMENTS

The work reported here was undertaken at the Imperial College of Science and Technology, London, during the tenure of a Commonwealth Public Service Overseas Scholarship, and is portion of a thesis submitted in part-fulfilment of the requirements for the degree of Ph.D. of the University of London. The author wishes to thank Dr. A. J. Rutter for his advice and helpful criticism throughout the course of the work.

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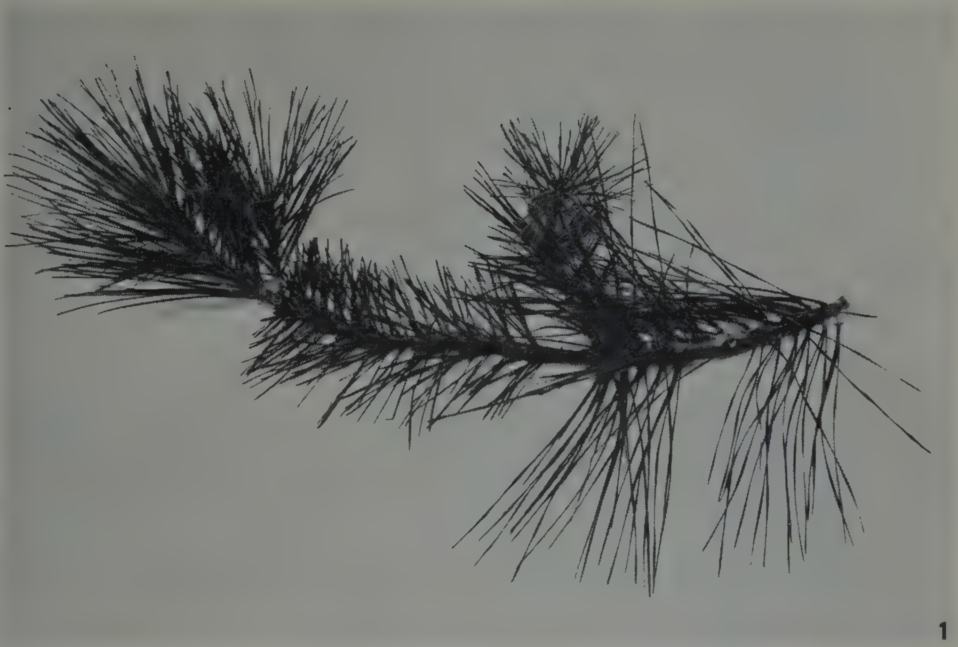

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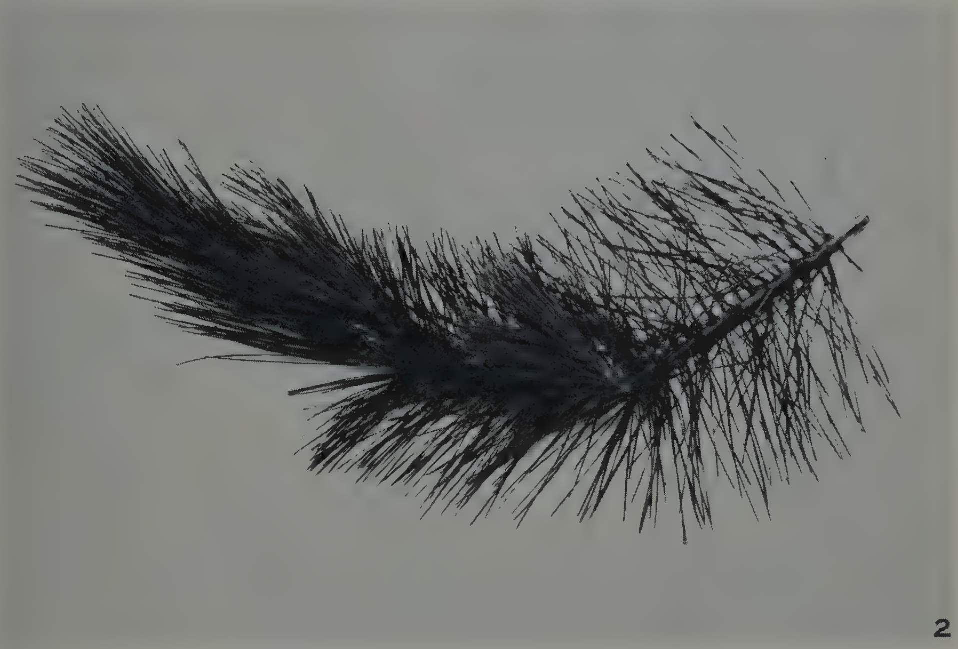
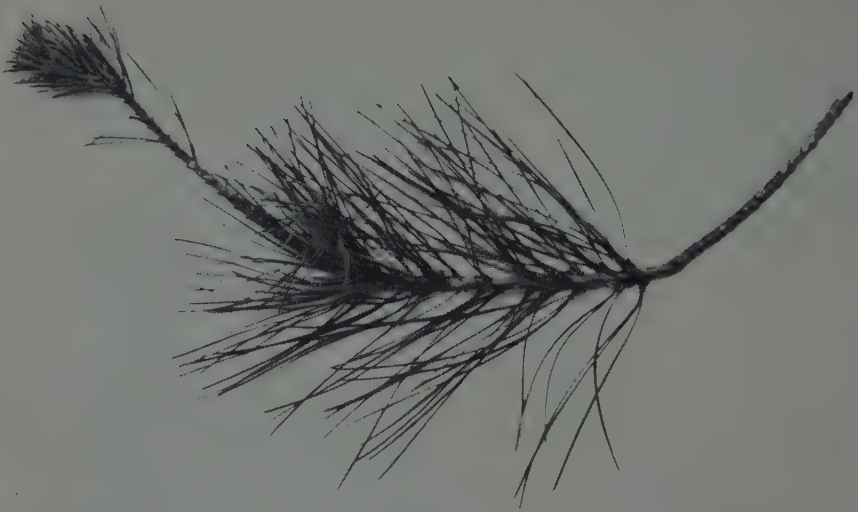


2

Effects of stem chilling on shoot growth.

Fig. 1.—Stem chilled to −4°C for 7 days. Needle length reduced during season of chilling; shoot length and needle number reduced in following season.

Fig. 2.—Control branch.



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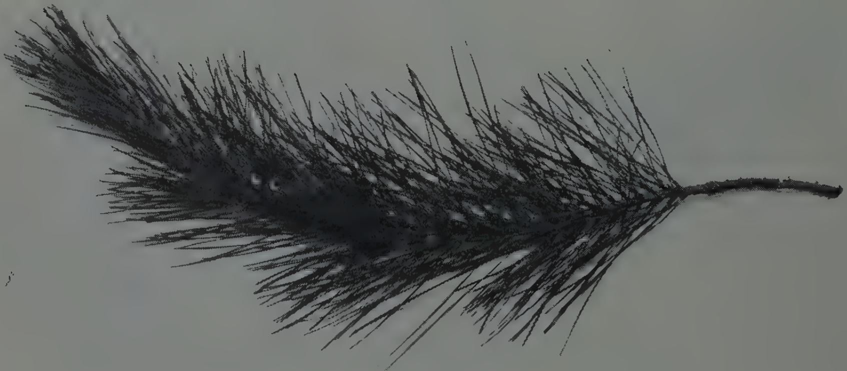

2

Effects of stem chilling on shoot growth.

Fig. 1.—Stem chilled to −6°C for 10 days. Most of current year's needles killed; shoot and needle growth greatly reduced in following season.

Fig. 2.—Control branch.

DEVELOPMENTAL MORPHOLOGY OF THE FLORAL ORGANS OF *EUCALYPTUS*

I. THE INFLORESCENCE

By D. J. CARR* and STELLA G. M. CARR*

[*Manuscript received January* 21, 1959]

Summary

The nature and structure of the inflorescence of *Eucalyptus* is re-defined in the light of an analysis of the unit inflorescence, its development, mode of branching, bract systems, and the grouping of unit inflorescences into compound inflorescences.

The structure of the unit inflorescence in 80 representative species is elucidated and a systematic notation for expressing the numbers and arrangement of the involucral bracts in dichasial inflorescences is proposed.

The inflorescence bud of *Eucalyptus* is generally asymmetrical in side view and often also in face view. External asymmetry is largely a result of the asymmetry of the outermost pair of bracts, by which the developing inner bracts and flowers are at first tightly enclosed, and may be reflected in an asymmetrical pattern of branching within the inflorescence. The asymmetry and pattern of branching are reflections of morphological features peculiar to the shoot system of *Eucalyptus*. The outer bracts resemble the adult leaves in their asymmetry about the midrib. The leaf and bract primordia arise decussately at the shoot apex but in most species the leaves of each pair become separated by the development of a segment of axis (an "intranode") between them.

In certain species the development of an intranode between the outer pair of bracts leads to the splitting apart or "disarticulation" of the unit inflorescence into two subclusters. The very complex inflorescence of *E. camaldulensis* arises by disarticulation of a simple inflorescence, followed by interpolation, in a centripetal manner, of additional bracts and flowers between those first formed. Flower numbers in clusters at successive nodes of the annual shoot may vary, rising with node number if the inflorescences are basitonically disposed, falling if acrotonically disposed. Flower number in successive clusters is correlated with other quantitative features of the annual shoot.

The position and number of the inflorescence buds on the annual shoot and the interval between flower initiation and anthesis are characteristic of species and of groups of species. Phylogenetic trends in inflorescence characters are discussed. Inflorescences with few flowers and with free persistent bracts, the number of which is related to the flower number in the cluster, are held to be primitive. Inflorescences with many flowers, fused bracts constituting a caducous involucre in which the number of bracts is not related to the number of flowers, are held to be advanced. These and other characters of the inflorescence are shown to have taxonomic significance and their use is typified in an analysis of the inflorescence characters of the Renantheroideae in relation to those of the Renantherae.

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I. INTRODUCTION

Because of the growing importance of the genus *Eucalyptus* in afforestation programmes all over the world, interest has been stimulated during the last 20 years in certain aspects of its systematics, genetics, and morphology. Despite the large volume of literature devoted to the genus, there appear to have been no developmental or comparative studies of its floral morphology. Such relevant observations as have hitherto been published will be mentioned in this series of papers on the structure and morphogenesis of the floral organs.

Pryor (1954) has briefly described the inflorescence of *Eucalyptus* in the light of the review by Rickett (1944) of the classification of inflorescences. Like those of previous authors (quoted by Maiden 1922–1923), Pryor's description is restricted, however, to the mature inflorescences of a very limited number of species and no account is given of the mode of development of the inflorescence. Pryor's main object was to point out that there may be irregularities in the inflorescences of hybrid forms, but he appears to have recognized irregularities only at some advanced state of maturity, either of the flowers or of the fruits. Even supposing that irregularities in the inflorescence are to be associated with hybridity, it is surely necessary to look to the development of the inflorescence for any explanation of their occurrence, because flower primordia may be lost from a variety of causes at any stage from initiation onwards. If further work is to be carried out on the inheritance of inflorescence characters in *Eucalyptus* in relation to hybridity, it is essential that closer attention be paid to the primordial stages. The material presented here is intended to amplify what has already been said by Pryor and to clarify certain aspects of the development of the inflorescence, but it would be futile to claim that it is in any sense a complete treatment of the subject. In a genus of over 500 recognized species (Blakely 1955) the possible range of variation is too wide to be encompassed by a brief account. In any case, certain aspects such as the time of development and the quantitative aspects of the inflorescence in relation to those of the annual shoot require much more prolonged and extensive study than we have been able to give them, and it is to be hoped that this publication will stimulate further work on these topics.

II. THE UNIT INFLORESCENCE

The unit inflorescence of *Eucalyptus* consists of three or more flowers arranged in a cyme, or of a single flower, and with few exceptions is axillary. Truly terminal flowers are found only in species with compound inflorescences such as are typical of the Corymbosae and of the Clavigerae (Maiden) S. T. Blake, in members of the Buxeales such as *E. hemiphloia* F. Muell., and in certain other species such as *E. pulverulenta* Sims and *E. camaldulensis* Dehn.*

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* As Rickett (1955) has pointed out, each flower may be considered as a terminal structure since, morphologically, the flower is a condensed shoot. The central, first-formed flower of a dichasium terminates the short shoot to which the axillary flower-cluster is morphologically equivalent. If, as will later be shown is the case in *E. camaldulensis*, the internodes within what is normally a contracted unit inflorescence become expanded, the terminal position of the central flower becomes emphasized. In this account "terminal" flowers are understood to be those which terminate a shoot with extended internodes, whether it is a "short" axillary shoot bearing no normal foliage leaves or a "long" shoot bearing normal leaves.

Any leaf may subtend an inflorescence but in any given species the inflorescences occupy a characteristic position on the annual shoot. In certain species the inflorescences are *basitonic*, i.e. it is the first-formed leaves of the annual shoot which subtend them (e.g. *E. cladocalyx* F. Muell., Plate 1, Fig. 1; *E. sideroxylon* (A. Cunn.) ex Benth., Plate 1, Fig. 2). In other species the inflorescences are *mesotonic*, i.e. subtended by the leaves formed at the height of the growing season (e.g. *E. lehmanni* Preiss., Plate 4, Fig. 1; *E. cinerea* F. Muell., Plate 2, Fig. 1), and in other species they are *acrotonic* and occupy nodes formed towards the end of the annual shoot (e.g. *E. saligna* Sm., Plate 2, Fig. 2; *E. hemiphloia*, Plate 8, Fig. 2).

The pattern of branching in the simpler cymes is dichasial, but in the more complex ones the initial dichasial system is succeeded by a monochasial system of branching.

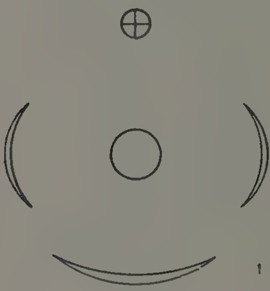
When it first appears in the axil of its subtending leaf the primordium of a unit inflorescence may be almost indistinguishable from that of an axillary vegetative shoot. The axillary shoot apex first gives rise to opposite leaf primordia and then, if it is determined as the apical meristem of a unit inflorescence, it gives rise directly to the successive whorls of a flower and further branching may be undertaken only by the axillary meristems of the two opposite leaf primordia, which have a truncated development and are determined as bracteoles. Their equivalents on a vegetative branch usually develop as deciduous prophylls (see Section V), but in some species (e.g. in the Cornutae) they become normal leaves, which at maturity are usually smaller than the later-formed leaves on the branch and may remain opposite or subopposite.

Inflorescence buds may readily be recognized when 1–3 mm long by the shortness of the bracteoles as compared with the equivalent leaf primordia of a vegetative bud of the same age, and by the relatively greater width of the inflorescence buds, due to the precocious development of the axillary meristems of the bracteoles, compared with vegetative buds. In species with solitary flowers the axillary meristems of the bracteoles remain suppressed, but in other species they develop by giving rise first to a pair of bracteoles and then to the successive whorls of a flower. It is customary to refer to the two leafy structures borne on the pedicel of a solitary flower as "bracteoles", but to an assemblage of such structures in a many-flowered inflorescence as an "involucre of bracts".

The flower buds of *Eucalyptus* are completely enclosed during the early stages of their development, while the floral whorls are being initiated, in an involucre of bracts. The individual bracts may be free or some, at least of the outer ones may be united in varying degree. In most species the bracts are shed while the flower buds are still comparatively small, but then the irregular ring of scars (Plate 7, Figs. 2, 3) persists and enlarges as the "common receptacle" of the flower cluster enlarges. The bracts have been referred to casually by various authors (cited by Maiden 1922–1923; Blake 1953) often as "bracts of the umbel" or as "the operculum of the umbel". The involucre has also been confused by some with the "double operculum" of the flower. Maiden himself fell into the opposite error by taking some of Mueller's (1879–1884) few records of "double opercula" as references to the presence of bracts. Neither Maiden nor Pryor (1954) appear to have understood fully the relationship between the bracts and the flowers. Maiden (1922–1923, Vol. 6, p. 466) believed that, potentially, each flower bud had a "bracteole", but that "bracteoles" were confined to members of the Corymbosae. Finding 14 bracts in the involucre of the seven-flowered dichasium of *E. ficifolia* F. Muell., Pryor seems to have assumed that of necessity each flower must have two bracteoles, which is certainly not the case. It is hoped that the following discussion and set of examples will help to clarify the situation.*

III. Bract Systems in Eucalyptus

In an axillary, cymose inflorescence each flower is normally subtended by a single bract which precedes it in development. In the simplest case, in which the inflorescence consists of a single flower, the leaf subtending it (its "Deckblatt" (Goebel 1931)) is its bract. This still remains true when this flower is no longer solitary, but occupies the central position in a dichasial or monochasial cluster. The pedicel of the flower may bear a pair of bracteoles ("Vorblätter", homologous with those of an axillary, vegetative branch) or a single bracteole. Following Troll (1957), it is convenient to refer to these bracteoles as "α" and "β", even when they appear to be strictly opposite and equal in size and development. When only one is present it is conventional to regard it as the α-bracteole.



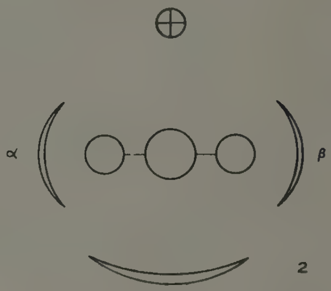


Fig. 1.—Inflorescence diagram of a solitary flower, subtended by a bract (or "Deckblatt"), the lowermost structure, and bearing two bracteoles on its pedicel.

Fig. 2.—Inflorescence diagram of a three-flowered cluster, the lateral flowers borne in the axils of bracts of series 2.

In those species of *Eucalyptus* in which the flower is solitary and axillary two opposite bracteoles occur on the pedicel (Fig. 1). They enclose the young flower bud, and the scar left after their abscission marks the junction of the flower with the peduncle, as in *E. globulus* Labill., (Plate 5, Figs. 3, 4), *E. macrocarpa* Hook., and *E. tetraptera* Turcz. In *E. stoatei* Gardn., as also in an unusual form of *E. globulus* which occurs at Toora (Vic.), the bracteoles persist at the base of the flower.

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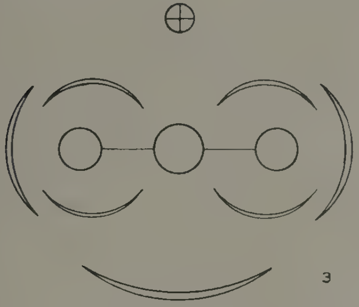
* The development and structure of the inflorescence has been examined in fresh material of representative species available in and near Melbourne. For other species, herbarium material has been examined by dissection and by hand and microtome sections, following a preliminary softening in 1 per cent. "Teepol". Information on many species not referred to in the text is included in Appendix I of this paper.

In a three-flowered inflorescence (Fig. 2) the central flower (1) is equivalent to the solitary axillary flower of the species mentioned above. The subtending leaf is its bract. Flowers of the second series (2) develop in the axils of the bracteoles of flower 1. In *E. tetrodonta* F. Muell., for instance, the inflorescence consists of three flowers with an involucre of two free bracts (the bracteoles of flower 1), which persist until the flowers open. In *E. viminalis* Labill., the involucre also consists of two bracts, but they are fused and fall as a cap, disclosing the three flowers. In other species in which the dichasia are three-flowered (e.g. *E. citriodora* Hook., and at least occasionally in *E. bicostata* Maiden, Blakely, & Simmonds) the pedicels



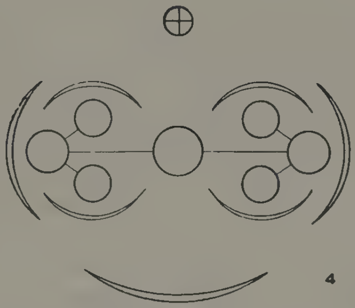
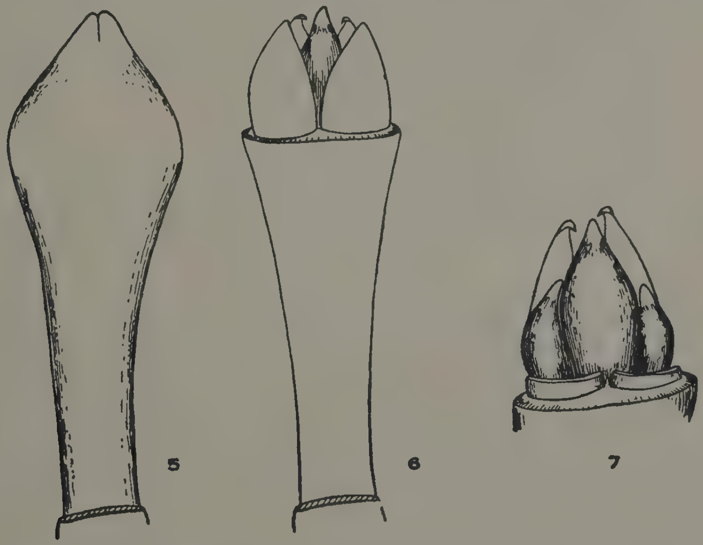


Fig. 3.—Diagram of a three-flowered cluster, with bracts of series 3 developed.

Fig. 4.—Diagram of a seven-flowered inflorescence, with an involucre of six bracts.



Figs. 5–7.—Inflorescence bud of *E. citriodora*. Fig. 5.—Anterior face of intact bud, showing fusion of outer pair of bracts. Fig. 6.—Outer pair of bracts removed to show four free inner bracts, surrounding the central flower. Fig. 7.—Anterior pair of bracts of series 3 removed to reveal the three flower buds.

of the flowers of series 2 each bear a pair of bracts (Fig. 3; Figs. 5–7). If the flowers of series 3 develop in the axils of the bracts borne on the pedicels of flowers of series 2, the inflorescence becomes seven-flowered (Fig. 4). In species in which the seven-flowered condition of the unit inflorescence is normal, the involucre may consist of 6 (Fig. 4), 14 (Fig. 8), or, by failure of the β-bracts of series 3 to form, of 10 bracts (Fig. 9). The unit inflorescence is commonly, but not invariably, seven-flowered in *E. calophylla* R. Br. and *E. ficifolia*, and in both species the number of involucral bracts varies between 10 and 14. These species are among the few in which the bracts frequently persist until the flowers are about to open, and the flower buds are never tightly enclosed by the involucre (Plate 6, Figs. 1, 2). Where there are 14 bracts, four of the bracts of series 4 occur within the flower cluster (Fig. 8). Where the number of bracts is 11, 12, or 13, the missing bracts are always internal members of series 4. It is probable that the frequent development of internal members of the bracts of series 4 in these species is related to the open character of the young inflorescence and a consequent lack of crowding. In many species in which the inflorescences are seven-flowered the involucre tightly encloses the flower buds and the internal bracts of series 4 do not develop. Indeed, even the external (α) bracts of series 4 may not be formed and the inflorescence then consists of seven or more flowers enclosed in an involucre of six bracts. Inflorescences of *E. saligna* may contain seven, nine, or eleven flowers surrounded by six, or up to ten, bracts, and in *E. gomphocephala* DC., the seven flower buds are enclosed by an involucre of six bracts. On the other hand, the internal bracts of series 4 may be suppressed but the external bracts of this and series 5 may develop, so that the new bracts are formed only to the outside of the cluster of flower primordia. This occurs in *E. cladocalyx*, in which the clusters are usually 11-flowered and there are 14 bracts

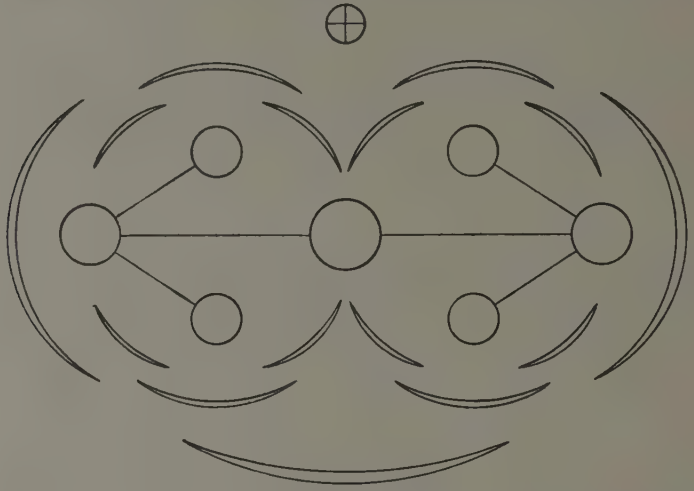


Fig. 8.—Diagram of a seven-flowered inflorescence with all the bracts of series 4 developed. The involucre has 14 free bracts. This and Fig. 9 illustrate structures common in buds of *E. ficifolia*.

(Fig. 10). The positions of the four extra flower buds in a 15-flowered cluster are indicated (by dotted lines) in Figure 10.

IV. Symmetry and Available Space in the Inflorescence Bud

To explain the development of dichasia with flower numbers greater than seven, Pryor (1954) postulates three possible systems, all of which involve the interpolation of flower primordia between others formed earlier. It is usually impossible for this to occur because in all but a few species the flower primordia develop, and in early stages are tightly packed, within the space enclosed by the bracts of series 2 and 3 (Plate 4, Figs. 3–6; Plate 7, Fig. 1). This space generally takes the form of a conoid of elliptical cross section with the short axis of the ellipse lying in the median (anterior–posterior) plane. Actually, the posterior side of this conoid is normally more flattened than the anterior (Plate 4, Fig. 5; Plate 5, Fig. 2).

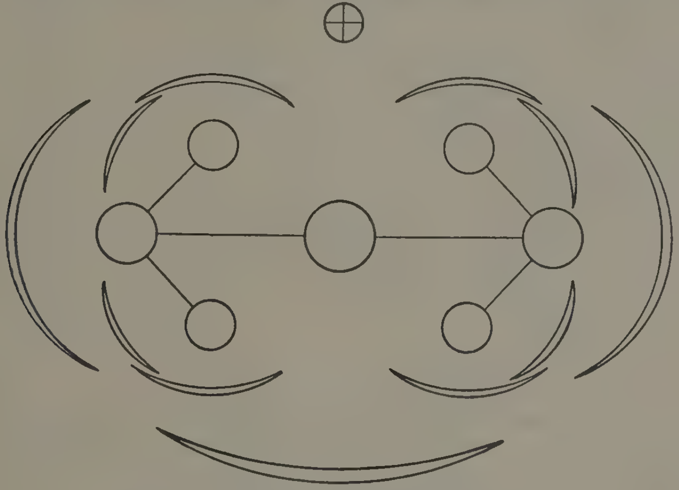


Fig. 9.—Diagram of a seven-flowered inflorescence with the four external bracts only of series 4 developed. The involucre has 10 free bracts.

The asymmetry of the inflorescence bud is not a mere consequence of pressure during its early development in the leaf axil, but is probably an expression of the inherent asymmetry of the shoot of *Eucalyptus*. In the juvenile condition the leaves are decussate and, on orthotropic shoots, symmetrical. Although in both juvenile and adult shoots the leaf primordia arise decussately at the shoot apex, in the adult condition one of each pair of primordia develops precociously. It enlarges more rapidly than the opposite primordium and becomes separated from it by the development of what may be termed an "intranode". Something similar to this occurs in the development of the first pair of leaves ("Vorblätter") of the vegetative axillary shoots of many dicotyledonous plants (Troll 1954), and a special term ("mesopodium") is used for the intranode which may develop between the initially opposite Vorblätter. In addition to the separation of the leaf pairs by the development of intranodes, there is a certain amount of twisting during the growth of the stem axis and petioles, so that the fully developed leaves come to lie more or less in one plane (Plate 1, Figs. 1, 2; Plate 2, Fig. 2). Like those of many other tree genera, the leaves of *Eucalyptus* are asymmetrical about the midrib. The adult leaves of many species, such as *E. obliqua* L'Herit., are markedly asymmetric and often falcate, but asymmetry can also be detected in leaves of species which retain the decussate phyllotaxis characteristic of the juvenile condition, and in leaves of "reversion shoots". The leaves of a pair are mirror images of each other so that, if falcate, the two leaves placed base to base form a crescent. The leaves above and below them on the same orthostichy are asymmetric in the same manner and direction, so that the successive pairs of leaves of a single shoot, viewed from its end, form two crescents at right angles to each other about the axis of the shoot. Although the asymmetry appears to be inherent in the shoot, and an expression of its dorsiventrality, experiment is required to show whether external factors may not be involved in its determination at the time of inception of the shoot apical meristem.

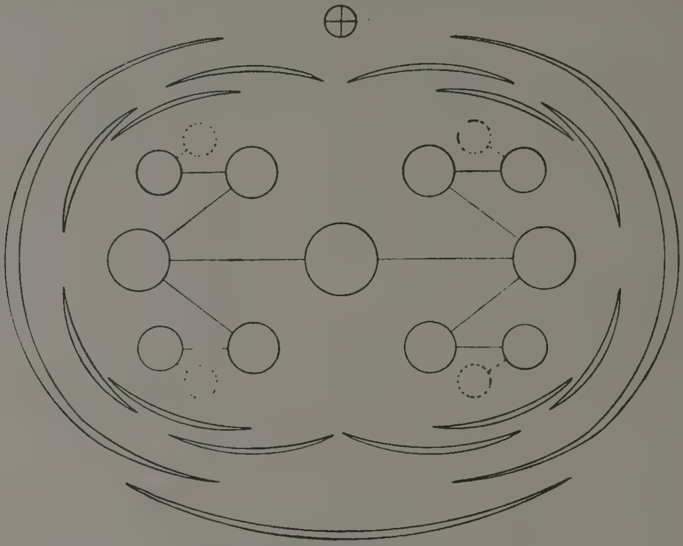
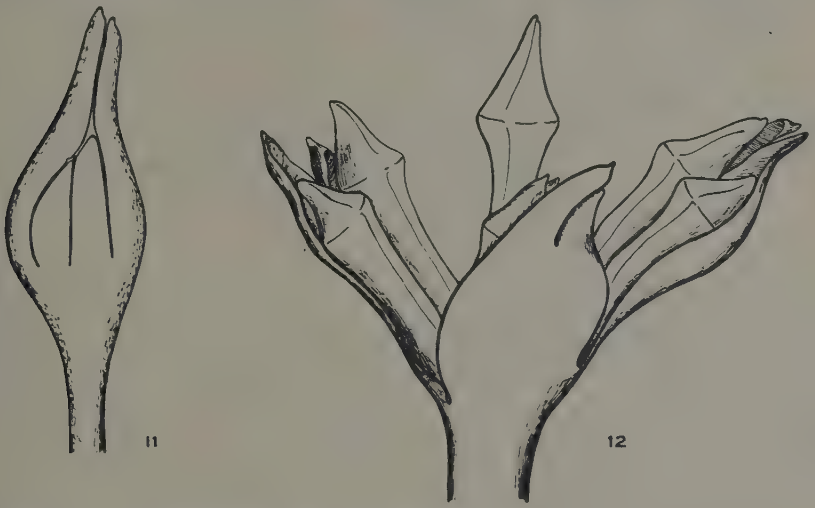


Fig. 10.—Diagram of an 11-flowered inflorescence with 14 free bracts in the involucre, as found, for instance, in *E. cladocalyx*. The putative positions of the next four flower buds, to make a 15-flowered inflorescence, are also shown.

The posterior halves of the two outermost bracts of the involucre (i.e. the bracteoles of the first flower) are smaller than the anterior, displaying the same kind of asymmetry as the foliage leaves. Since these two bracts are largely responsible for determining the shape of the inflorescence bud, the latter is asymmetric in the anterior–posterior plane (i.e. in side view, Plate 2, Fig. 2). One of the two bracts is often slightly larger than the other (Plate 2, Fig. 1; Figs. 11, 12) and may be designated as the α-bract. When this is the case the inflorescence bud is asymmetric also in face view (Plate 6, Fig. 3). On the more orthotropic shoots of species or forms with decussate phyllotaxis the inflorescence buds are not noticeably asymmetric (e.g. forms of *E. cinerea*, Plate 2, Fig. 1).

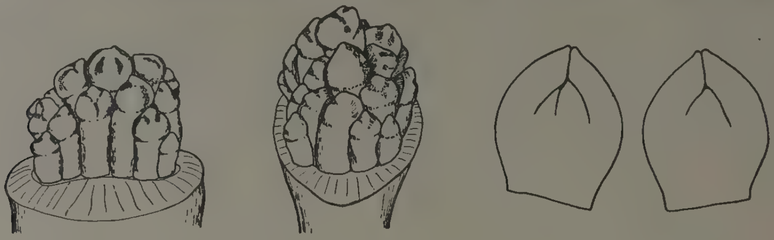
All the flower primordia are laid down before there is any indication that the involucre is about to be shed. The primordia are not initiated simultaneously but centrifugally in successive series and, while retained within the involucre, the flower buds remain graded, the oldest and largest in the centre, the youngest and smallest at the circumference of the cluster (Plate 6, Fig. 2; Plate 7, Fig. 1; Figs. 13–16). The bracts also form a graded series, but the oldest and largest are the outermost. Except in such species as *E. calophylla*, *E. ficifolia*, and the seven-flowered forms of *E. sideroxylon*, in which the inflorescence is open from an early stage, bracts are never found within the cluster of flower primordia but are external to it. This rule implies that bracts and flower primordia cannot be formed between previously developed flower primordia in an inflorescence tightly enclosed by an involucre. They appear to be initiated only where there is space for their subsequent development. In certain species the unit inflorescences often become "disarticulated" by the development of some of the internodes between the flowers. In these cases, which are dealt with in Section VIII, disarticulation is accompanied, in its more extreme forms, by the formation of "internal" bracts.



Figs. 11, 12.—Inflorescence buds of *E. macrorrhyncha*. Fig. 11.—Anterior face of intact bud, showing four of the six free involucral bracts. Fig. 12.—The inflorescence bud viewed from the posterior face shortly after opening. Note the fusion of the posterior pair of bracts of series 3 and the asymmetry of the inflorescence bud in face view.

V. Branching Systems and the Number of Flowers in Unit Inflorescences

The pattern of branching of the inflorescence is uniformly dichasial up to the seven-flowered condition, and the involucre of a seven-flowered inflorescence invariably consists of at least six bracts (two of series 2, four of series 3) either separate or fused in varying degree. In species in which the number of flower buds in the inflorescence is either three or seven this number may be adhered to with great regularity. In species in which the flower number varies, the sequence of flower numbers changes in successive clusters along the annual shoot in a fairly regular and predictable manner, following closely the variations in other quantitative features of the annual shoot, such as the lengths of successive internodes and leaves. Some data for two representative species are shown in Figure 17 and Table 1.



Figs. 13–16.—Inflorescence buds of *E. radiata*. Figs. 13, 14.—Involucre dissected away to reveal the flower buds viewed from the anterior face (Fig. 13) and from the side (Fig. 14). Figs. 15, 16.—The intact inflorescence bud, to show the greater degree of fusion of the posterior bracts of series 3. Fig. 15.—The anterior face. Fig. 16.—Posterior face of the same bud.

In some inflorescence buds the abnormal numbers may be traced to loss of one or more primordia consequent upon insect attack, but in most cases there is no evidence of loss of flower buds by injury, and the abnormal condition is evidently due to the complete absence of flower primordia from certain positions in the flower cluster. The frequencies of flower numbers in clusters of *E. kitsoniana* (J. G. Lueh.) Maiden (Plate 3, Fig. 2) from southern Victoria and *E. saligna* are given below. These were determined from dissections of 113 undamaged inflorescence buds of *E. kitsoniana* and 58 of *E. saligna*.

	E. kitsoniana							*E. saligna*				
No. of flower buds in cluster	1	2	3	4	5	6	7	7	8	9	10	11
Frequency (%)	0	0·9	5·3	12·3	6·2	9·7	65·5	25·6	30·6	22·5	12·2	8·6

These frequencies do not appear to occur in a simple Poisson series or any other simple series.

Along any selected annual shoot the lengths of the successive internodes increase up to a maximum and then decrease. If the mean lengths of successive internodes are plotted the resultant graphs are somewhat bell-shaped and resemble the curves of quantitative features of successive organs of annual plants, supposed by Krenke and others to be diagnostic of "physiological ageing" (Ashby 1948). The leaves subtending the most proximal and the most distal internodes are unlike the foliage leaves; they shrivel and are shed after reaching a length of 1 or 2 cm and a width of a few millimetres. They fail to develop marginal meristems and correspond developmentally to the solid tips ("Vorläuferspitze" (Troll 1954)) of the normal leaves. Despite the possibilities of misinterpretation surrounding the use of the term "prophyll" (Rickett 1954) we propose to use it to describe these deciduous leaf-structures in *Eucalyptus*. In *E. saligna* the first four nodes and the last three or four of the annual shoot generally bear prophylls.

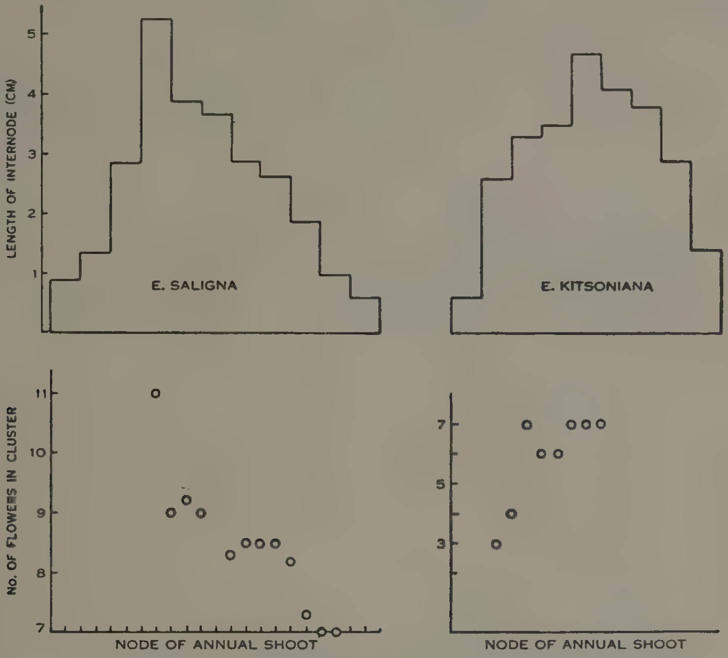


Fig. 17.—Lengths of the internodes (grouped in pairs) and numbers of flowers in clusters at successive nodes of *E. saligna* (means of 10 annual shoots) and *E. kitsoniana* (a single annual shoot). The internodes were measured to the more distal node of each cognate pair, and each measurement thus comprises an internode and an intranode.

Just as the lengths of successive internodes increase, so also in species with basitonically disposed inflorescences (e.g. *E. kitsoniana*) the flower number at successive nodes increases, and the last-formed cluster has the maximum number of flowers. In species with acrotonically disposed inflorescences the flower number in successive clusters falls with the falling length of the internodes, so that it is the first-formed cluster which has the maximum number of flowers, and the last-formed has the minimum number (e.g. *E. saligna*; see Fig. 17). Clusters with the smallest flower numbers are generally associated with very small internodes and are usually subtended by prophylls (Table 1).

Champagnat (1954*a*, 1954*b*) has reached the conclusion, from extensive studies of the growth and morphology of the annual shoots of European trees and shrubs, that the number and vigour of axillary shoots which develop depend largely on a "size factor" which may generally be described as the "vigour" of the mother shoot.

He has put forward experimental evidence to show that the factors regulating the activity of the axillary buds are nutritive rather than hormonal. The position of branching, whether acrotonic, basitonic, or mesotonic, is a characteristic of the species and is not affected by changes in nutrition or vigour. Although Champagnat's work is concerned mainly with the vegetative development of axillary meristems, his conclusions may be of some interest in considering the features of the annual shoot of *Eucalyptus*. They suggest that the flower number in each cluster reflects the vigour of growth of the shoot at the time when the flower primordia are being initiated. If, as Champagnat concludes, the vigour of growth of the annual shoot reflects its nutritive status then the flower number may also be determined by the same factor. Evidence from observations on vigorous coppice shoots of *E. pauciflora* Sieb. supports this contention. Whereas the normal flower number in the material we have examined of this species is 15, rapidly growing coppice shoots of the same trees may bear inflorescence buds with over 60 flower primordia (Figs. 18, 19).

TABLE 1

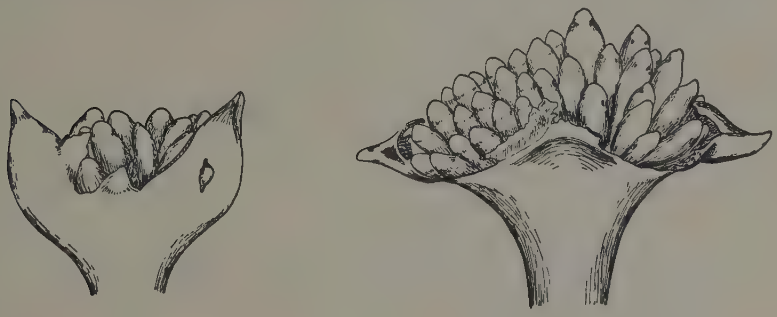
ANALYSIS OF THE LEAVES AND INFLORESCENCE BUDS OF THE SUCCESSIVE NODES OF 10 ANNUAL SHOOTS OF E. KITSONIANA

Node on Annual Shoot	Frequency Ratios		Numbers of Inflorescences with Following Numbers of Flowers in the Clusters						
	Prophyll to Leaf	Vegetative to Flowering	1	2	3	4	5	6	7
1	10 : 0	10 : 0							
2	10 : 0	9 : 1						1	
3	9 : 1	4 : 6			1	1		1	3
4	8 : 2	0 : 10		1	1		1		7
5	5 : 5	1 : 9			2		1		6
6	3 : 7	0 : 10			1		2		7
7	0 : 10	0 : 10			1	2			7
8	0 : 10	0 : 10					2	2	6
9	0 : 10	0 : 10					1	2	7
10	0 : 10	0 : 10					1	1	8
11	0 : 10	4 : 6						1	5
12	0 : 10	6 : 4						1	3
13	0 : 10	8 : 2							2
14	0 : 10	10 : 0							

15th and successive nodes up to 20 all vegetative and bearing normal leaves

Despite the fact that Pryor (1954) has observed abnormal numbers of mature flower buds or fruits in a small proportion of the inflorescences of a known hybrid (*E. rubida* Deane & Maiden × *maideni* F. Muell.) and has suggested that "it may be taken as a rule that the presence of three-flowered clusters in the basal position of a single shoot . . . (which elsewhere bears seven-flowered clusters) . . . indicates hybridism" there are no grounds for the supposition that the material we have examined of *E. kitsoniana* (Table 1) originated from hybrid trees. It is not impossible that hybrids between parents having dissimilar flower-bud numbers may exhibit the phenomenon mentioned by Pryor, but it seems impossible to accept that this phenomenon demonstrates hybridity, unless it is supposed that similar variations in other quantitative features of the annual shoot also demonstrate hybridity.

Species in which the clusters are more than seven-flowered may display a considerable range of variation in the number of flowers. Unit inflorescences of *E. radiata* Sieb. (near Melbourne) are most frequently 15-flowered, and inflorescences with 9, 11, or 13 flowers are common. The sizes and positions of the buds within the involucre provide evidence that after the seven-flowered stage the pattern of branching is monochasial, but may show some irregularities. The branching pattern may be modified to fit, as it were, the space available within the involucre. In *E. dives* Schauer, for instance, clusters of 19 buds are of common occurrence, possibly following the series 1, 3, 7, 11, 19, but in other clusters the bud numbers do not conform to a regular series. Figures 20 and 21 are diagrams of the branching patterns by which clusters of 21 and 23 buds were developed. That illustrated by Figure 20 was a very asymmetrical inflorescence and the bracts on the left-hand side of the bud appeared to have suffered some damage at an early stage. The inflorescence illustrated by Figure 21 had an involucre which was very much flatter on the posterior than on the anterior face. Both cases illustrate modifications of the branching pattern to fit the space available within the involucre. Another example of the same kind is that of the seven-flowered form of *E. sideroxylon*, mentioned above. Some of its inflorescences are nine-flowered, the extra flowers being the anterior members of series 4, external to those of series 3.


18 19

Figs. 18, 19.—Inflorescence buds of *E. pauciflora* shedding their involucres. Early (Fig. 18) and late (Fig. 19) stages in bract shedding.

VI. Bract Fusion

In certain species the bracts are fused except at their tips. In species of the section Renantherae (Blakely 1955) (for instance, *E. radiata*, *E. dives*, *E. obliqua*, *E. pauciflora*, and *E. regnans* F. Muell.), the involucre consists only of the six outermost bracts (two of series 2 and four of series 3), although the number of flowers in the unit inflorescences of these species may be much larger than seven. The degree of fusion of the bracts may be somewhat variable, even within the species. In some buds of *E. radiata*, for instance, the tips of the anterior bracts may be discernible (Figs. 15, 16), but in other buds they are not. Bract fusion is carried to its extreme in species such as *E. vitrea* R. T. Baker. In that species the participation of six separate bracts in the formation of the involucre can only be deduced from the presence of the lines of cuticle representing the small and contiguous free tips of the bracts at the top of the somewhat globular inflorescence bud.

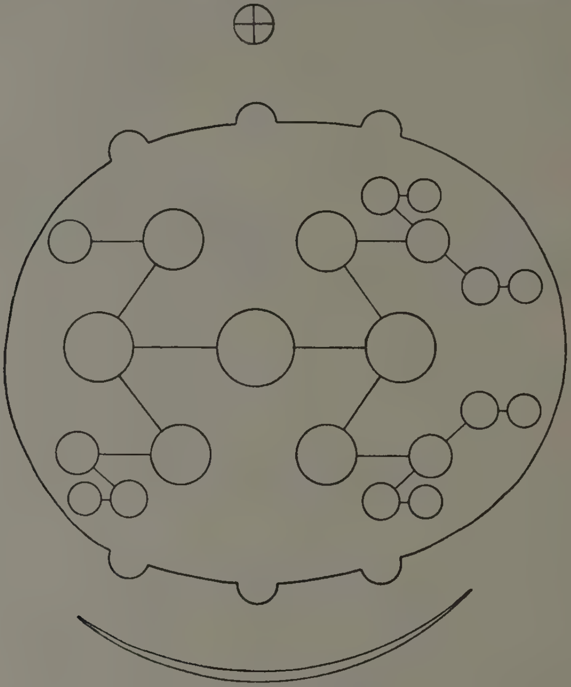


Fig. 20.—Diagram of inflorescence of *E. dives*.

One of the most striking cases of bract fusion occurs in *E. lehmanni*, in which the involucre consists largely of the six outer bracts of which only the extreme tips are free (Plate 4, Figs. 3–5). In addition to these, some of the bracts of series 4 and even of series 5 may be formed, but these are totally enclosed in the outer envelope of fused bracts, and are readily recognizable by their free tips only in early stages of development (while the involucre remains green). The whole of this bract system, which thus consists of six outer and from two to ten inner bracts, is shed as a large cap (Plate 4, Figs. 2, 6). Fusion is only slightly less pronounced in the related *E. cornuta* Labill., and here too the involucre, which consists of six outer bracts and eight free, inner bracts, is shed as a cap. The two species included in the series Miniatae (Blakely 1955), *E. phoenicea* F. Muell. and *E. miniata* A. Cunn., both have involucres consisting of six fused bracts, which are apparently shed as a cap in the same manner as that of *E. lehmanni*. Those of *E. miniata* are well illustrated but wrongly interpreted by Gardner (1954).

Fusion is always more pronounced on the posterior side of the inflorescence (Figs. 11, 12; 15, 16). This is another expression of the inherent asymmetry of growth of the inflorescence about an axis at right angles to the median plane. In many species of the Renantherae, the anterior pair of bracts of series 3 may be readily recognized by their free tips, but the posterior pair may be so completely fused as to form a single structure. In certain seven-flowered forms of *E. sideroxylon*, and in *E. macrorrhyncha* F. Muell. and its near relatives in the Renantherae, the two bracts of series 2 and the anterior pair of series 3 are usually free, but the posterior pair of series 3 are often fused. In species such as *E. lehmanni*, in which the involucre is shed as a cap, the asymmetry is further emphasized at the time of shedding of the involucre because this process is initiated by a split which develops on the anterior face of the bud (Plate 4, Figs. 2, 4, 6). The flower buds quickly enlarge and protrude through this split, which widens and spreads around to the posterior face.

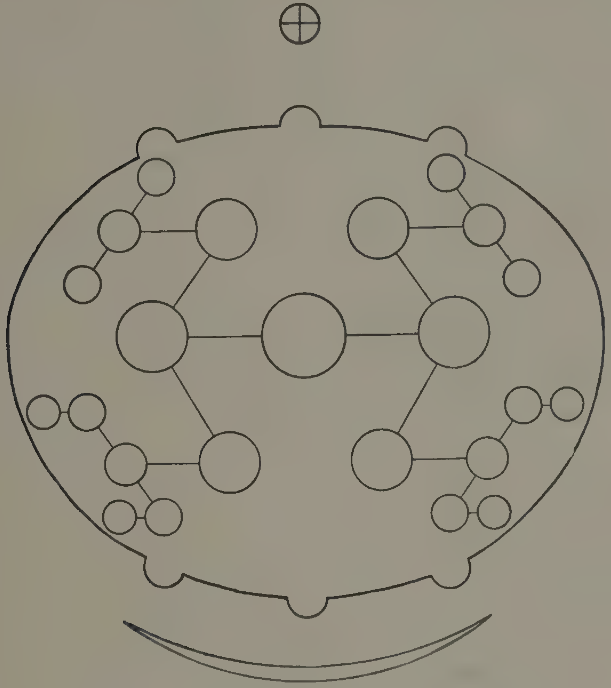


Fig. 21.—Diagram of inflorescence of *E. dives*.

In some species, particularly those of the Cornutae, including *E. lehmanni*, *E. cornuta*, and *E. platypus* Hook., an asymmetry of growth of the strap-shaped peduncle is also evident. The inflorescence is initially erect (Plate 4, Fig. 1), or even incurved, but on approaching maturity an epinastic curvature begins, due to excess growth of the adaxial face of the peduncle, and the inflorescence becomes deflexed. This curvature does not result from the asymmetry of the flower cluster because the peduncle of the unrelated *E. stoatei* (a single-flowered species) also becomes deflexed. Although, in *E. lehmanni*, the curvature is most rapid about the time of shedding of the involucre, deflexion is not necessarily connected with that process because it begins before it. Moreover, in *E. stoatei* the bracteoles persist; they become curved around the pedicel, clasping its abaxial face.

VII. Bract Shedding

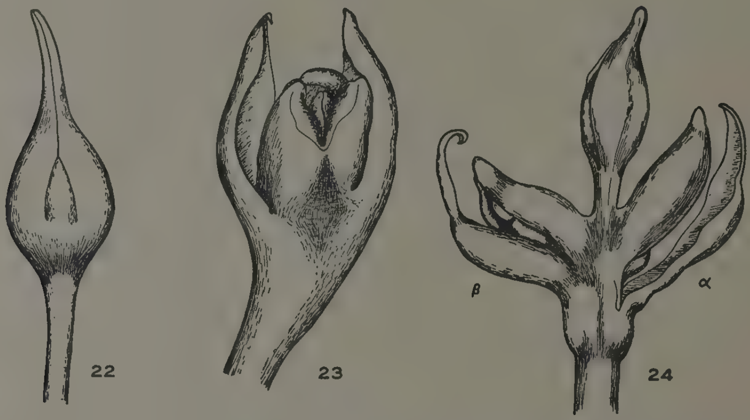
Up to the time when the involucre is shed the flower buds show marked differences in size (Plate 7, Fig. 4), but all are at about the same stage of development and have the primordia of all the floral whorls. Except in cases specially mentioned above (e.g. *E. ficifolia*, *E. calophylla*) all the bracts of the involucre are shed at about the same time. Even if not actually fused, the margins of the two outermost bracts and, where present, those of the four of series 3, are closely contiguous in early stages of development of the inflorescence bud, but later they separate (Plate 5, Figs. 1, 3; Plate 6, Figs. 3, 4). Separation of the lower parts of the bracts of series 2 may take place during the development of the inflorescence, so as to accommodate the bracts of series 3 (Plate 6, Fig. 3), but the tips remain contiguous. At the time of opening of the inflorescence buds the bracts, if free, are bent back about their line of insertion (Plate 6, Fig. 5) and immediately begin to shrivel. In species with fused bracts the involucre may be shed as described above for *E. lehmanni*, or by an irregular tearing, up the middle of the anterior and posterior faces and around the base. The shrivelled involucre may then be carried up as a cap on the expanding flower buds or it may be separated into two irregular parts, borne outwards on the tips of the flower buds (Figs. 18, 19). When the involucre opens or is shed the orientation of the flower buds changes. The buds, which previously have been constrained to point inwards, or at least to be erect, now turn outwards (Plate 1, Fig. 1; Plate 7, Figs. 2, 3). The opening of the inflorescence buds is due to a sudden decline in the growth rate of the bracts of the involucre relative to that of the flower buds. Prior to this the growth rates of the bracts are matched with that of the flower buds, so that the involucre remains intact while the whole inflorescence bud is enlarging. It seems likely that in many cases the actual spreading of the bracts is brought about by pressure due to the outward curvature of the flower buds, which generally remain closely appressed to the spreading bracts (Fig. 12; Plate 6, Fig. 5).

Bract shedding occurs relatively early in the development of many species, when the flower buds are not longer than 2–5 mm. The bracts may be shed within a few days from the majority of the inflorescence buds of a given tree. It seems likely that it is for this reason that inflorescence buds with intact involucres are not often represented in herbarium material, have rarely been included in published illustrations, and have not been adequately described. Baker (1900) even erected a species ("*E. polybractea*") after observing the bracts in specimens of some already described species (supposedly *E. fruticetorum* F. Muell.) in process of opening their inflorescence buds and shedding the bracts. Once the involucre falls or opens, the smaller flower buds grow very rapidly, and long before the buds reach full maturity the differences in size between the oldest and youngest become slight (Plate 1, Fig. 1; Plate 2, Fig. 2). The flowers in any one inflorescence usually reach maturity together and open about the same time.

VIII. Compound Inflorescences

The unit inflorescence which has been described in the foregoing is always an unbranched, axillary structure and, therefore, a *simple* inflorescence. This type of inflorescence is characteristic of the majority of species of *Eucalyptus*. A compound inflorescence may result from the grouping of a number of unit inflorescences to comprise either a lateral, branched structure or a terminal one. The position of the compound inflorescence, whether terminal or lateral, has been used by Blake (1953) as a taxonomic criterion to distinguish between the series Clavigerae and the series Corymbosae. In *E. latifolia*, for instance, the inflorescence may terminate a "long shoot" (i.e. a shoot bearing a number of normal leaves). The shoot apex becomes a flower bud and each of the two divergent, persistent bracts below it subtends a cluster of three flowers. On the other hand, in *E. papuana* (Clavigerae) the unit of the compound inflorescence is a short lateral shoot which bears no normal leaves and which terminates in a single flower. Below this flower such a shoot bears a number of decussately arranged flower clusters each subtended by a deciduous prophyll. The death and abscission of the terminal vegetative bud of a long shoot bearing a number of lateral compound inflorescences like those of *E. papuana* gives the whole branch the appearance of a twice-compound inflorescence, referred to as a corymb and often described as terminal. To avoid confusion between truly terminal, compound inflorescences and those which become pseudo-terminal by loss of the distal, vegetative parts of the long shoot, it would seem better to distinguish between those inflorescences which terminate long shoots and those which terminate short shoots. The Clavigerae would then be distinguished from the Corymbosae in that the inflorescence in the latter may terminate a long shoot. On this basis, however, *E. citriodora* and *E. maculata* Hook. (normally included in Corymbosae) would not accord with the rest of the group, because their compound inflorescences terminate only short shoots. Blake (1953) agrees that these two species "depart somewhat from the general trend in having usually axillary corymbose panicles". In fact the compound inflorescence of these species is a raceme of cymes or, more correctly, a thyrsus, and is not corymbose.

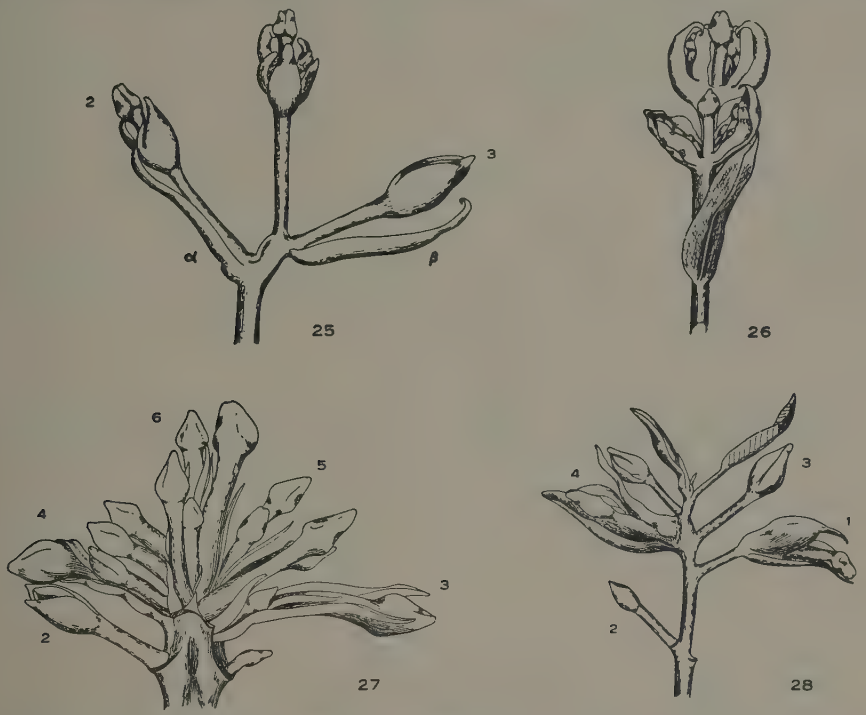
Truly terminal inflorescences are almost entirely restricted to species of the Corymbosae and Clavigerae and the series Buxeales, Melliodorae, and Heterophloiae (boxes and mallee boxes) (Blakely 1955). In *E. hemiphloia* (grey box) the inflorescences are produced towards the end of the annual shoot and consist for the most part of axillary, seven-flowered clusters with 10 free bracts. The prophylls which subtend these clusters are shed while still primordial and the inflorescence buds open and lose their involucres of free bracts when the flower buds are only 1–2 mm long. The annual shoot which gives rise to these inflorescences eventually terminates as a flower bud. The intranode between the last pair of prophylls to be initiated (which are really the bracteoles of the terminal flower) extends, separating the flower buds in their axils into two separate clusters. The phenomenon can perhaps be understood by reference to the splitting apart or *disarticulation* of a normal cluster of seven flowers into a group of three and a group of four flowers, which occurs unusually by growth of the intranode in *E. sideroxylon* (Plate 7, Fig. 4). In *E. hemiphloia* and allied species the early elongation of the intranode enables one or more bracts and flower primordia to be laid down adjacent to the flanks of the terminal flower. Thus, instead of a terminal group consisting of two clusters, one of three and one of four flowers, together with 10 bracts (i.e. a normal seven-flowered cluster split into two parts), it is more usual to find a lower cluster of three or four (with six bracts) and an upper one of four, five, or six flowers, with six bracts. Thus the whole terminal group, with the central terminal flower, consists of eight to eleven flowers.



Figs. 22–24.—Inflorescence buds of *E. camaldulensis* in different stages of opening. Figs. 22 and 24.—Viewed from the posterior face.

The most complex inflorescences are undoubtedly those of *E. camaldulensis*. The axillary inflorescence buds appear (in Melbourne) at the beginning of November at the proximal nodes of the new annual shoots. In early stages they bear an outward resemblance to the unit inflorescence of most species of *Eucalyptus* (Fig. 22), completely enclosed by two outer bracts which are parted at their bases to reveal the bases of structures formed apparently by fusion of the anterior and posterior pairs of bracts of the next series. This appearance is, however, deceptive. Each of the outer bracts (α and β) potentially subtends a small unit inflorescence (1 and 2). They become separated by the development of an intranode between them (Figs. 23–25). The structures resembling the paired and somewhat fused bracts of series 3 (in a normal unit inflorescence of other species) also separate during development, the zone of fusion at the base being drawn out until it resembles the web between a thumb and index finger. Each anterior and posterior pair forms a hood covering a flower cluster (clusters 3 and 4). Finally, there is a central cluster with a terminal flower and two lateral groups (5 and 6) which may each be one- or three-flowered (Figs. 25–27). Inflorescences borne on the more distal nodes of the annual shoot may bear a vegetative bud instead of the central terminal flower (Fig. 28) but commonly the vegetative apex aborts after having produced one or two leaves. As in other species of *Eucalyptus*, one or two of the more distal nodes may also have a small, simple inflorescence, the product of an accessory bud situated in the same leaf axil as the main bud, but abaxial to it.

The apparently simple inflorescence bud of *E. camaldulensis* is thus highly complex. Its complexity is enhanced by the exigencies of space within the separate flower clusters which constitute it. The first flowers to develop are the central flowers of the terminal and lateral clusters (3 and 4). The inflorescence buds which may be borne in the axils of the α- and β-bracts usually remain small and often one of them is not formed at all. As the whole compound bud grows, space in the lateral clusters becomes available in a centripetal direction and the remaining five or six flowers of clusters 3 and 4 (as well as those of 1 and 2) develop centripetally (Figs. 27, 29). The bracts of series 3 and some of series 4 are developed within the lateral and subterminal inflorescence buds, and, like the bracts which surround the whole compound inflorescence, they remain free (Fig. 29). Within the lateral



Figs. 25–28.—Inflorescence buds of *E. camaldulensis*. Figs. 25, 26.—Face and side views respectively of a single inflorescence. Note the intranode which has developed between the α- and β-bracts, and the long peduncle of the central clusters (5, 6, and the terminal flower). Fig. 27.—Face view of a contracted group of clusters. The α- and β-bracts have been shed, revealing the axillary clusters 1 and 2 (the latter very small). The bracts external to clusters 3 and 4 have been shed but the internal bracts of these and of the terminal clusters are shown. Fig. 28.—An inflorescence bud terminating in a vegetative shoot. Cluster No. 1 has become displaced upwards from the axil of the bract and is larger than normal. Cluster No. 6 is replaced by a vegetative bud, axillary to a leaf.

clusters, then, the flower buds and their bracts form a graded series, the larger situated towards the outer part of the cluster, the smaller towards the central axis of the compound inflorescence (Fig. 27).

This complex structure might be regarded as derived either from excessive condensation of a lateral, compound inflorescence, such as that of *E. ficifolia*, or by an elaboration of the process of disarticulation described above for the terminal flower clusters of *E. hemiphloia*. We are inclined to the latter view because of similarities such as the arrangement of the bracts of series 3, inserted at right angles to those of series 2, "in pair" and not decussately "in tandem", and the centripetal insertion of bracts and flower primordia in the developing lateral and subterminal flower clusters. These clusters, when fully developed, may have five, six, or seven flowers. However, it is possible to regard clusters 1 and 2 as derived from accessory buds of bracts α and β, of which the main buds give rise to clusters 3 and 4.

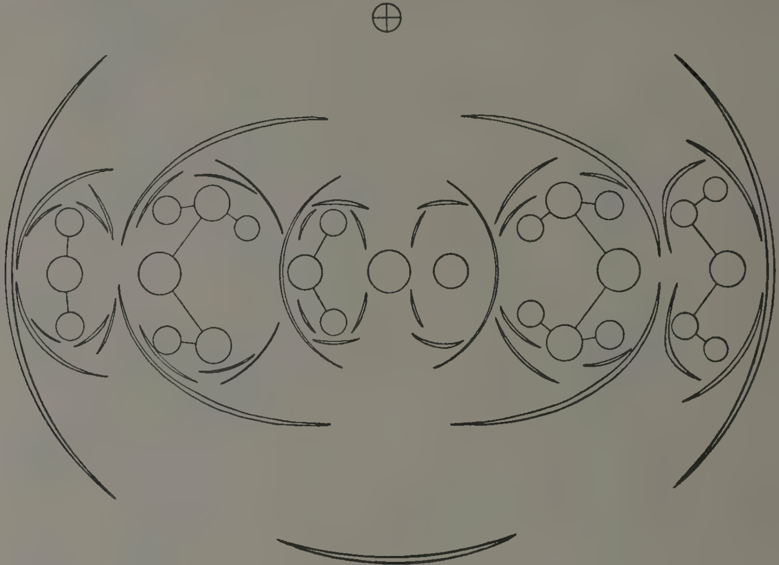


Fig. 29.—Diagram of a representative inflorescence bud of *E. camaldulensis* with 26 flower primordia.

As far as can be judged, the potential maximum number of flower primordia in the whole compound inflorescence of *E. camaldulensis* is between 25 and 35, but by no means all of the primordia present in early stages reach maturity, and of those which do, relatively few give rise to mature fruits. The shape of the inflorescence at maturity depends on the degree of separation of the unit inflorescences (Figs. 25, 27, 28). If they remain close together (Fig. 27) the compound inflorescence may simulate a simple one containing a large number of flower buds. Indeed, it is usually quite impossible to detect, in the mature inflorescence or even in one from which the bracts have been shed, the whole of the complex arrangement described above. This complexity has been observed in inflorescence buds from different trees in different localities in Victoria and also in material collected in

Queensland and New South Wales. The inflorescence buds of species supposed to be closely related to *E. camaldulensis*, namely, *E. rudis* Endl. and *E. tereticornis* Sm. syn. *E. umbellata* (Gaertn.) Domin, are apparently simple, but we have been able to dissect only a few buds of each. However, an examination of herbarium material and of buds freshly collected from trees of "*E. studleyensis* Maiden", reputed to be a hybrid between *E. camaldulensis* and *E. ovata* Labill., shows that whatever may be the true identity of these trees, they have simple inflorescences.

In addition to the types of compound inflorescence described above, there are cases in which two simple inflorescences are brought together by abortion of intervening parts of the shoot to form a falsely compound inflorescence. In *E. crucis* Maiden the axillary inflorescences are usually three-flowered, but some, apparently terminal, inflorescences are to be found which are six-flowered (Plate 7, Fig. 3; Plate 8, Fig. 1). These six-flowered inflorescences are formed by abscission of the axis distal to two axillary three-flowered clusters, which then become apposed to form a compound inflorescence superficially resembling a seven-flowered inflorescence which has lost one bud from series 2 or 3. This appearance is enhanced by the fact that, during development, one of the flower buds comes to occupy the approximate centre of the cluster (Plate 8, Fig. 1). The six-flowered and superficially terminal inflorescences of *E. caesia* Benth. and of *E. cinerea* are produced in the same manner. In many species of *Eucalyptus* the terminal buds of many of the lateral branches appear to abort, after inflorescence buds have been produced on these branches during their first or second year of growth. It is in species or forms with decussate phyllotaxis (such as those mentioned above) that this abortion leads to the production of an apparently regular, terminal flower cluster.

IX. Discussion

(*a*) *Phylogenetic and Taxonomic Importance of Inflorescence Characters*

The three-flowered condition characteristic of the unit inflorescences of species of Eudesmieae has been generally regarded as primitive (Blake 1953). On this view advance has thus taken place in two directions: (*a*) towards reduction in the number of flowers in the cluster to one; (*b*) increase in the number of flowers in the cluster to seven or more. Other features of the inflorescence may be regarded as having undergone phylogenetic change in the evolution of the genus. Thus, the primitive species may have had free bracts which persisted at least until the flower opened (as in *Angophora* and in *Eucalyptus setosa* Schau. and *E. tetrodonta*), and, taking into account the subtending leaf, at least one bract for each flower of the cluster. The phylogenetic trend appears to have been towards the fusion of the bracts in varying degree and the shedding of the bracts at a relatively early stage in the maturation of the flowers, as well as towards reduction in the number of bracts until no strict relationship holds between the number of bracts in the involucre and the number of flowers in the cluster.

For example, in the Corymbosae, which on other grounds are held to be somewhat primitive eucalypts, some advance on the three-flowered condition with free, persistent bracts is evident. *E. calophylla* and *E. ficifolia* show advance in the number of flowers in the cluster but retain the persistent bracts and their numerical relationship to the number of flowers. Other species of the Corymbosae (e.g. *E. citriodora*) have the outer pair of bracts fused, while the inner ones remain free; or, like *E. papuana*, lose their bracts at a relatively early stage in the maturation of the flower buds. The species included in the series Miniatae by Blakely (*E. miniata* and *E. phoenicea*) have inflorescences showing all the most advanced features. Although the flower clusters in *E. phoenicea* may contain as many as 22 flowers (*E. miniata* has fewer) the involucre contains only six bracts, which are fused except for their extreme tips.

The inflorescence characters of the species grouped by Blakely as the Renantheroideae and Renantherae are of particular interest. These groups, although largely composed of clearly and obviously related species, nevertheless contain species the affinities of which are doubtful. Blakely has divided the Renantherae into two groups, Renantherae and Renantherae-Normales. In the latter two main types of inflorescence buds can be distinguished, that characteristic of the stringybarks (e.g. *E. macrorrhyncha*, Figs. 11, 12) and that characteristic of the snow gums (e.g. *E. pauciflora*, Figs. 18, 19) and peppermints (e.g. *E. radiata*, Figs. 13–16). *E. macrorrhyncha* has long, pointed inflorescence buds with six free bracts with rather fleshy tips, and seven to eleven flower buds. The two outermost bracts are unequal and well separated at their bases, exposing the four shorter bracts of series 3. The posterior pair of these may show some fusion but the anterior is not fused. When the inflorescence buds open, the bracts are splayed by the expanding flower buds, which are characteristically long and angular from mutual compression and have a long, tapered operculum.

The inflorescence bud of the snow gums and peppermints is characteristically enclosed in six fleshy bracts, fused except at their tips. The number of flower buds is usually more than seven and may be over 60. The bracts are shed by tearing up the anterior–posterior mid-lines and along the base, and the torn halves of the shrivelled involucre are separated by the expanding flower buds (Fig. 19). Those species of Blakely's series Fraxinales which we have been able to examine (*E. gigantea* Hook. f., *E. sieberiana* F. Muell., *E. consideniana* Maiden, *E. kybeanensis* Maiden & Cambage) all have six bracts, fused except at the tips. Within the Renantherae-Normales, then, there appear to be two types of inflorescence bud which may be designated as the "stringybark type" and the "peppermint type". The former has six free bracts which separate in a regular fashion when the inflorescence bud opens. The peppermint type has six fused bracts shed by irregular tearing. There is some gradation in the degree of fusion of the bracts, which reaches its maximum in the snow gums (e.g. *E. vitrea*). On the basis of the inflorescence characters the stringybarks may be regarded as retaining primitive features while the peppermints and snow gums are more highly advanced.

Of the other group in the Renantherae we have examined material of *E. sepulcralis* F. Muell., *E. buprestium* F. Muell., and *E. marginata* Sm., the most important species of Blakely's "series Occidentales". *E. sepulcralis* has seven- to eleven-flowered inflorescence buds on very long peduncles, and six bracts, fused except at their tips. The involucre is in the form of a parallel-sided and rather flattened sleeve, 2–3 mm long at the time it is shed. Shedding takes place by transverse splitting at the base of the involucre. *E. buprestium* and *E. marginata* also lose their bracts at a relatively early stage, but of these species we have not seen young inflorescence buds with the bracts intact.

On the basis of anther characters certain species are placed by Blakely close to the Renantherae, in the section Renantheroideae. Of these species we have been able to examine material of *E. pachyloma* Benth., *E. diversifolia* Bonpl., and *E. todtiana* F. Muell. *E. pachyloma* has a globular inflorescence with seven flower buds totally enclosed in six free and very fleshy bracts which are shed while the flower primordia are still relatively small. The involucre in this species is unusual in that the four inner bracts (series 3) form a complete envelope around the flower buds and are themselves tightly and completely enclosed by the two outer bracts (series 2). *E. todtiana* has seven-flowered buds resembling very closely those of the stringybarks. *E. diversifolia* also has seven- to nine-flowered inflorescence buds of the stringybark type, and the seven-flowered buds of *E. patens* Benth. also appear to be of this type. On the basis of inflorescence characters, therefore, it would appear that at least some of the species of the section Renantheroideae may have affinities with the stringybarks. On the other hand, *E. sepulcralis*, and possibly other members of the series Occidentales, have inflorescence buds more akin to those of the peppermints.

Within the Renantherae-Normales at least one species is included by Blakely which, on the basis of the inflorescence characters alone, is sufficiently unlike the other members of this group to suggest that it should be placed elsewhere in the systematic arrangement. This is *E. microcorys* F. Muell., which has terminal, paniculate, rapidly maturing inflorescences which are quite unlike those of the other members of the Renantherae. It is clear from a statement by Maiden (1922–1923, Vol. 6, p. 332) that he realized that this species, placed by Mueller (1879–1884) in the Renantherae on the basis of its anther characters, should not be included in that group. However, Maiden died before assembling his evidence, and in the posthumous volumes *E. microcorys* is always treated as belonging in the Renantherae. On the basis of its dorsiventral leaves, its inflorescence, and other characters, *E. microcorys* should be placed in Blakely's series Transversae (Macrantherae). As a corollary, if, as Pryor suggests (1956), hybridization can only take place between species of the same or related anther groups, it should be impossible to make the hybrids between *E. microcorys* and cold-resistant species of Renantherae (*pauciflora*, *kybeanensis*, etc.) which he recommends (Pryor 1956).

The peculiar and distinctive features of the inflorescence of *E. camaldulensis* are not found, as far as our limited information goes, in other members of its series (Exsertae), which has always been regarded as a fairly natural group of species. It is perhaps unfortunate that closer attention was not paid to the features of the inflorescence at the time of the controversy over the synonymy of this species (Osborn 1937). It is impossible to judge, from the photograph published by Osborn of the type specimen, which appears to have only clusters of fairly mature flowers, whether its inflorescences are simple or compound. It will be necessary to examine the specimen at first hand in order to make certain that its inflorescences match those of the trees which have come to be designated, with some reluctance, in Australia as "*E. camaldulensis*".

A feature of the inflorescence which appears to be of some taxonomic and phylogenetic significance is the period of time between initiation and opening of the flowers. In other genera of the Myrtaceae (e.g. *Angophora*, *Tristania*) the flower primordia are laid down in the winter bud and the flowers open within a few weeks or months of the resumption of growth in early summer. In many species of *Eucalyptus* also, the time taken for full development of the flower buds is less than 1 calendar year. In *E. sideroxylon*, for instance, the full cycle of development takes about 9 months. In *E. calophylla* and *E. ficifolia* a period of about 6 months or less elapses between initiation and opening of the flowers. On the other hand, the flower buds of *E. camaldulensis* require about 13 months for their full development.

Species of the Renantherae which, as we have seen, display other features of advance as far as the inflorescence is concerned, appear to be advanced also in that the flower buds may take 2 or even 3 years from initiation to opening. The buds of *E. radiata* are initiated at the distal nodes of the annual shoot in January–February (near Melbourne), the bracts are shed in the following December when the buds are still only 1–2 mm long, and the flowers open about a year later. Other species known to conform to this pattern are *E. pauciflora*, *E. regnans*, *E. consideniana*, *E. stellulata* Sieb., and *E. dives*. In *E. regnans* and *E. alpina* Lindl., the full cycle of development may take 3 years. This apparently advanced feature of slow maturation of the flowers is also found in members of the Cornutae, e.g. *E. lehmanni* and *E. cornuta*. In the Corymbosae, also, some species have a long cycle of development. The flower buds of *E. citriodora* take 22–24 months from initiation to opening.

The number and position of the inflorescence buds on the annual shoot, together with the relative dominance of the leader shoots, play a large role in determining the shape of the mature tree. In many species of the Corymbosae, for instance, the annual shoot is of determinate growth, the inflorescences occupy a pseudo-terminal position, and branching is undertaken by vegetative axillary shoots of the proximal nodes. These shoots in their turn behave like their parent shoots. It is this habit which gives rise to the much-branched, compact shape of well-grown trees of species such as *E. calophylla* and leads to their use in street plantings. On the other hand, species such as *E. papuana* ("ghost gum"), in which the annual shoots are of indeterminate growth and the inflorescence shoots account for most of the lateral branches, which are eventually shed as clusters of fruits, are trees of an open habit and long, relatively unbranched limbs.

The potentiality for almost every axillary bud on an annual shoot to give rise to an inflorescence is shown in a number of species, such as *E. stellulata* and *E. kitsoniana*, but in most species the production of inflorescence buds is restricted to the proximal, intermediate, or distal nodes on the annual shoot. One may thus distinguish certain types of arrangement of inflorescences along the annual shoot, characterized by selected species, and in many cases typical of taxonomic groups.

In the "*cladocalyx*" type, inflorescence buds occupy the axils of deciduous prophylls on the proximal nodes of the annual shoots. The shedding of the bracts and, eventually, the fruits, leaves the lower parts of the annual shoots completely bare, and branching can be undertaken only by axillary shoots of the distal nodes. These branches do not develop more than a few vegetative nodes after initiating inflorescences on their proximal nodes, and subsequent to maturation of the fruits, are shed leaving the main axis bare. It is this combination of deciduous prophylls, axillary inflorescences, and caducous lateral branches which give rise to the characteristic "dish-mop" appearance of the limbs of *E. cladocalyx.* As a variant on this, in the "*globulus*" type the inflorescences are subtended, not by prophylls, but by normal foliage leaves (Plate 3, Fig. 1). The retention of the leaves on the proximal parts of the annual shoot after flowering, together with the longer life of the vegetative branches, results in a more leafy appearance than is the case with *E. cladocalyx.* In the "*saligna*" type the inflorescences are developed from the axillary buds distal on the annual shoot, while in the "*cinerea*" type the inflorescences are mesotonic on the annual shoot, the first two or three nodes being vegetative as well as the distal nodes. In *E. cinerea* and *E. saligna* branching takes place from the last node or nodes produced on the annual shoot.

The number of inflorescences produced on an annual shoot may be almost as great as the total number of nodes or it may be reduced to a few or even to one. In the ironbarks, for instance (e.g. Plate 1, Fig. 2), between two and six proximal inflorescences are produced, occupying usually fewer than half of the total number of nodes of the annual shoot. In *E. lehmanni* (and other members of the Cornutae) the number of inflorescences on the annual shoot may be reduced to one or two, occupying an intermediate, somewhat proximal position (Plate 4, Fig. 1).

It is fairly characteristic of the Renantherae that the inflorescences are produced on the distal parts of the annual shoot (e.g. *E. radiata*, *E. consideniana*). This may contribute to the slowness of flower development in these species owing to the cessation of development during the period of dormancy which follows shortly after the initiation of the buds. It is essential, however, that this brief résumé of the position and duration of development of the inflorescence should be amplified by field observations over a number of years. It seems likely that conditions of temperature and possibly also of photoperiod may affect the initiation and subsequent rate of development of inflorescence buds in *Eucalyptus.* Whereas the nutritional status of the shoot may be involved in determining the number of flowers in the clusters, a hormonal control, mediated by environmental conditions, may be involved in determining axillary meristems as inflorescence primordia. Indeed, the extraordinary degree of branching and leafiness of some species of *Eucalyptus* grown in North America (see Jacobs 1955) may be no more than an expression of failure, in certain environments, to initiate inflorescence primordia and of the production of additional vegetative shoots.

(*b*) *Systems of Dichasial Branching in* Eucalyptus *Inflorescences*

Pryor (1954) has postulated three developmental series of bud numbers, as follows:

(*a*) 1, 3, 7, 11, 15, 23, 35 . . .
(*b*) 1, 3, 7, 13, 21, 31 . . .
(*c*) 1, 3, 7, 15, 31 . . .

He recognizes that, for instance, *E. pauciflora* conforms to his series (*a*) as far as 15, but does not anywhere admit the possibility of an inflorescence containing 19 flowers. It has been shown earlier that this number does occur (e.g. in *E. dives* and *E. radiata*) and that it is derived either by purely monochasial development after the seven-flowered stage (giving the series 1, 3, 7, 11, 15, 19) or by the interpolation of a single monochasial step (7–11) in an otherwise regular dichasial system, i.e. 1, 3, 7, 11, 19. The regular mode of branching has not been determined beyond this stage in the series.

Considering Pryor's series (*b*) it appears that the number 13 is more commonly derived by incomplete development of the buds of the fifth series, giving the sequence 1, 3, 7, 11, 13. Similarly, 21 can originate from the series 1, 3, 7, 11, (? 15), 19, 21 with incomplete development of the sixth or seventh series of buds. It is most unlikely that Pryor's series (*c*), a complete and regular dichasium, is ever realized in the contracted and asymmetrical inflorescence characteristic of most species of *Eucalyptus* because of the limitations of space imposed by the crowding of the earlier series of flower buds within the involucre.

In some species of *Eucalyptus* the pattern of branching involved in the development of the flower clusters can be identified on the basis of the number of extra bracts formed at successive stages beyond the seven-flowered condition. This is especially true of the compound inflorescences of *E. camaldulensis*, the nature and pattern of which are only decipherable while the bracts are present. On the other hand, despite the large number of flower buds characteristic of many species of the Renantherae (e.g. *E. radiata*), no bracts beyond series 3 are produced. However, the seriation of the flower buds can be determined, while the buds are still enclosed in the involucre, by their relative sizes and pattern of arrangement.

The number of flower buds in the cyme just prior to anthesis is often much smaller than the number of primordia originally laid down. Buds are lost at all stages owing to mechanical injury, insect attack (even while the involucre is still tightly closed), and other causes. For this reason, and also because the actual number of flower primordia formed in different inflorescence buds of one tree or even of one branch may vary, any statements about the true nature of the inflorescence or the number of flower buds it contains must be based on studies of the developing inflorescence, with particular reference to stages when the involucre is still present. The importance of such developmental studies cannot be overemphasized and, if the inflorescence of *Eucalyptus* is considered in this way, it is obviously preferable to refer to the single axillary flower of certain species not as "the ultimate stage of reduction from an indefinite dichasial cyme, which would be preceded by a three-flowered cyme" (Pryor 1954), but as an inflorescence which has failed to branch. Even from the point of view of phylogeny, Pryor's statement would be misleading.

(*c*) *Nomenclature*

In discussing the term "dichasium", Rickett (1955) states that it would seem best to reserve the term for the following meaning: "A peduncle bearing a terminal flower and two bracteoles, which subtend lateral flowers. A repetition of this sort of branching from the axils of the bracteoles of the lateral peduncles forms a compound dichasium." Rickett adds: "It would seem unnecessary to coin special terms for the various complex systems which may ensue; since the plan is fundamentally that of a dichasium, the term compound dichasium may embrace them all, unless the transition occurs at the first branching."

The dichasia in *Eucalyptus* are commonly referred to as umbels and we agree with Pryor (1954) in accepting Rickett's suggestion that the definition of the term "umbel" (as well as those of "capitulum", "panicle", and "corymb") should be widened to include sympodial as well as monopodial forms. There is no justification, however, for extending the term umbel to include cases, e.g. *E. lehmanni*, *E. cornuta*, and *E. neglecta* Maiden, in which the flowers are sessile. In Blakely's (1955) description of the genus, adopted without acknowledgment from Bentham (1866), the inflorescences are described as umbels or heads, but in Blakely's species descriptions he invariably refers to the inflorescences as umbels.

In view of the difficulty of deciding in some intermediate cases whether the inflorescence is an umbel or a capitulum, it seems best to refer to the unit inflorescences as "flower clusters" when they contain three or more flowers. The descriptions "flowers in threes", "clusters seven-flowered", etc. are sufficiently explicit because, by definition, the branching system of the inflorescence is dichasial. In view of the inadequacy of the existing definitions of the inflorescence of *Eucalyptus*, the following is put forward as a basis: "Unit inflorescence a solitary flower, supported by two bracteoles, an open or contracted dichasium, or a contracted compound dichasium. Unit inflorescence stalked or sessile. Young flower clusters surrounded by a deciduous involucre composed of the free or united bracteoles of the terminal flower and those of the other flowers of the cluster. Flower clusters with the form of umbels or capitula (heads). Flowers usually free, rarely united. Unit inflorescences solitary in the axils either of vegetative leaves or of deciduous bracts on the main axis, or arranged on leafless lateral branches or terminating long shoots, forming racemes. By loss of the subtending bracts, and, in those species in which the racemes occupy lateral branches, by death of the terminal bud of the main axis, the inflorescences may be grouped as leafless panicles, which are sometimes aggregated to form corymbs."

X. ACKNOWLEDGMENTS

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EXPLANATION OF PLATES 1–8

PLATE 1

Fig. 1.—Annual shoot of *E. cladocalyx* a few days after the opening of the inflorescence buds. The inflorescences are subtended by prophylls, which have been shed, on the proximal nodes of the shoot. Note the pair of transitional leaves at about the middle of the shoot.

Fig. 2.—Annual shoot of *E. sideroxylon* at the time of opening of the inflorescence buds. Except for the most proximal, these buds are borne in the axils of foliage leaves. Note the small number of inflorescence buds and their long bracts.

PLATE 2

Fig. 1.—A branch of *E. cinerea* just prior to the opening of the inflorescence buds on the new annual shoots. The inflorescence buds are borne in the axils of leaves about the middle of the annual shoot, as shown by the position of the fruits on the annual shoot of the previous year. Branches are produced from the most distal nodes of the annual shoot. In the photograph the uppermost pair of branches has grown in the current year, the lowermost pair began to grow last year. The tip of the lower branch has begun to abort and it will eventually be shed, leaving this branch with a pseudo-terminal pair of inflorescence buds.

Fig. 2.—A 3-year-old branch of *E. saligna*, prior to resumption of growth. The fruits are situated towards the end of the annual shoot of the first year, and no leaves of that year are now present. The following year, no flowers were formed and only four leaves of that year remain. Towards the end of this second year's growth, the lateral branch was initiated. In the third year the flowers and the remaining leaves were formed. Vegetative buds were also formed in the axils of the prophylls (which have been shed) subtending the most distal internodes.

PLATE 3

Fig. 1.—Annual shoot of *E. globulus*, showing solitary flowers in the axils, except for the lowermost, of foliage leaves. The three more proximal flower buds have shed their bracts. Compare with Plate 5.

Fig. 2.—Incompletely developed annual shoot of *E. kitsoniana* with large inflorescence buds with their involucres intact. The more proximal inflorescences are borne in the axils of prophylls which have been shed. The distal nodes of the annual shoot are vegetative.

PLATE 4

E. lehmanni

Fig. 1.—Part of an annual shoot, with a single inflorescence bud and two developing lateral branches. The inflorescence bud is in the axil of the second leaf shown (actually the fifth on the annual shoot).

Fig. 2.—An inflorescence bud, with its subtending leaf, at the time of shedding of the involucre. Note the free tips of the involucral bracts, the split developing on the anterior face of the bud, and the epinastic curvature of the peduncle.

Figs. 3, 4.—Posterior and anterior aspects respectively of an inflorescence bud shedding its involucre. On the anterior face the flower buds are beginning to protrude through the slit. On the posterior face abscission of the involucre is imminent.

Fig. 5.—Inflorescence bud viewed from its free end, showing the marked fusion of the bracts and the anterior–posterior asymmetry of the inflorescence bud.

Fig. 6.—An inflorescence bud with the involucre almost shed, exposing the enlarging flower buds.

PLATE 5

E. globulus

Fig. 1.—Inflorescence bud viewed from the anterior face.

Fig. 2.—The same, viewed from the side. To the left, the axis, to the right the subtending leaf.

Fig. 3.—Anterior face of an inflorescence bud, shedding its bracts.

Fig. 4.—The solitary flower, after bract shedding. Note the scars of the bracts at the top of the pedicel.

PLATE 6

Fig. 1.—Anterior face of an inflorescence bud of *E. calophylla*, showing the two bracts of series 2 and the anterior pair of series 3. Note the openness of the inflorescence bud.

Fig. 2.—A slightly older bud than that shown in Fig. 1, with the anterior pair of bracts of series 3 excised to display the flower buds. The central flower bud is the largest; it is flanked by two flower buds of series 2, and in front of it are the two smaller flower buds of series 3. Between these and on their flanks the very small bracts of series 4 are visible.

Fig. 3.—Anterior face of intact inflorescence bud of *E. cladocalyx*, showing the two outermost bracts, contiguous at their tips, but parted at the base to reveal the anterior pair of bracts of series 3. All the bracts remain free.

Fig. 4.—Posterior face of intact inflorescence bud of *E. pauciflora*, in which all the bracts are fused.

Fig. 5.—Inflorescence bud of *E. kitsoniana*, shedding its involucre. The expansion of the flower buds has caused the six fused bracts to become torn up the middle of the anterior and posterior faces. The scar at the bottom of the peduncle is that of the prophyll which subtended it.

PLATE 7

Fig. 1.—Transverse section of the upper part of the inflorescence bud of *E. gigantea*, anterior face below, posterior above. The section shows the close packing and consequent angularity of the flower buds, tightly enclosed in the bracts, of which only the outer pair of series 2 is evident. Because of the exigencies of space within the asymmetrical inflorescence bud, the posterior pair of flower buds of series 3 are much smaller than the anterior pair, and are not cut in the section. Because of size differences, the flower buds are cut at different positions along their length.

Fig. 2.—Flower cluster of *E. gomphocephala* just after bract shedding. One bract is still present on the left. Note the change in orientation of the flower buds after loss of the involucre, and the scars left by the bracts.

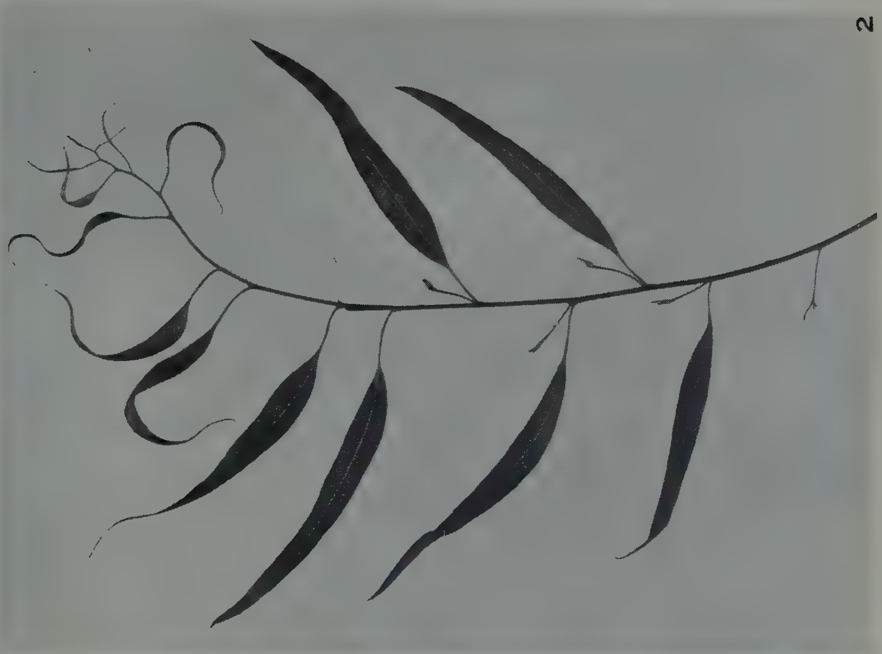
Fig. 3.—Flower cluster of *E. crucis*. Note the shrivelled pair of bracts at the base of the pedicels. Compare with Plate 8, Fig. 1.

Fig. 4.—Flower clusters of *E. sideroxylon*, a day or two after emergence from the bracts. On the left, a normal cluster; note the very long pedicel of the central flower and the differences in sizes of the six other flowers. On the right, a "disarticulated" flower cluster, showing the development of an intranode separating the cluster into a three-flowered cluster, and an upper, four-flowered cluster. The central flower is recognizable by its relatively great length.

Plate 8

Fig. 1.—Pseudo-terminal flower cluster of *E. crucis*, with six flowers. Note the scar marking the position of the abscised terminal shoot.

Fig. 2.—Annual shoot of *E. hemiphloia*, showing the development of a compound, pseudo-terminal inflorescence. The unit inflorescences are borne in the axils of prophylls on short lateral shoots, the more proximal of which retained their apical buds and are thus potentially capable of further, vegetative growth as "long shoots". Other short lateral shoots each end in a terminal flower-cluster. By loss of the remaining leaves and most or all of the growing points, the whole branch system becomes converted into a compound, paniculate inflorescence.



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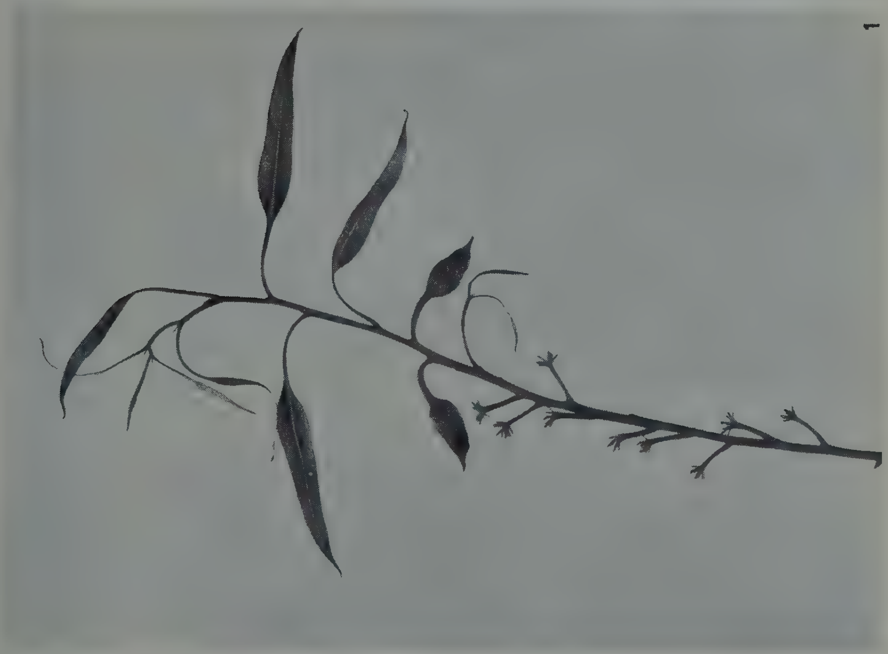

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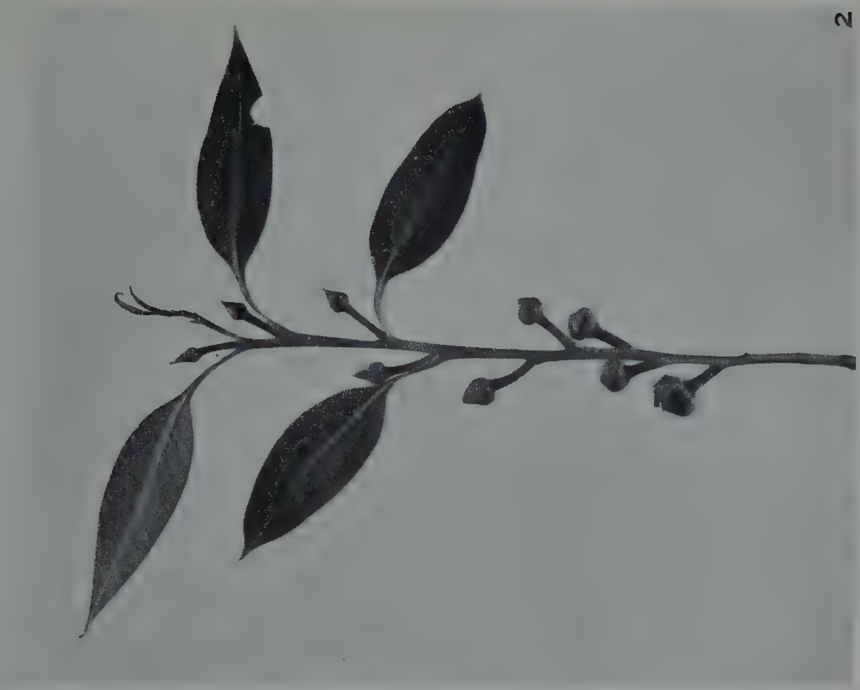

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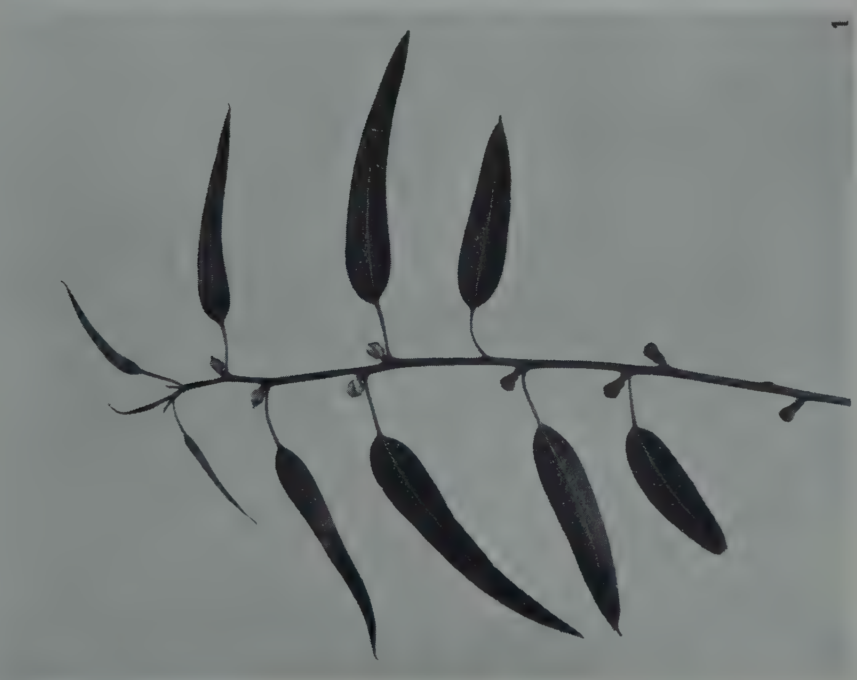

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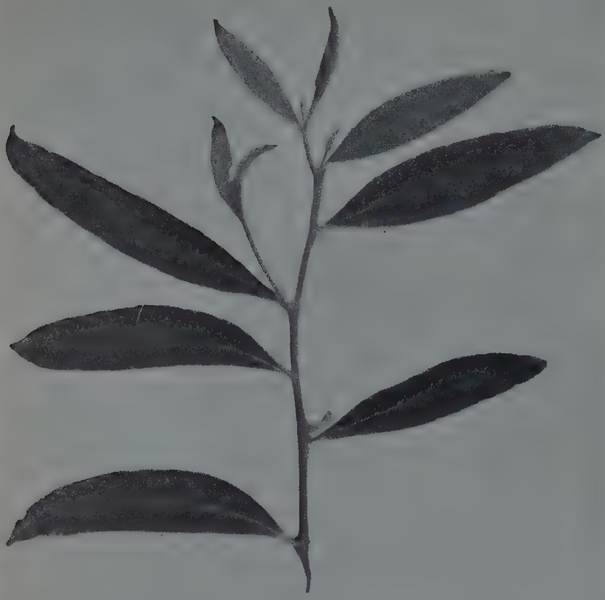
Plate 4

MORPHOLOGY OF FLORAL ORGANS OF EUCALYPTUS. I



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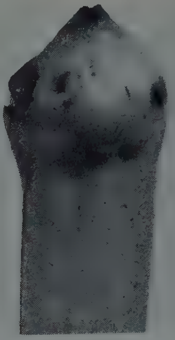

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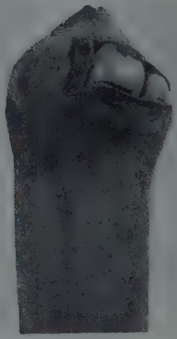

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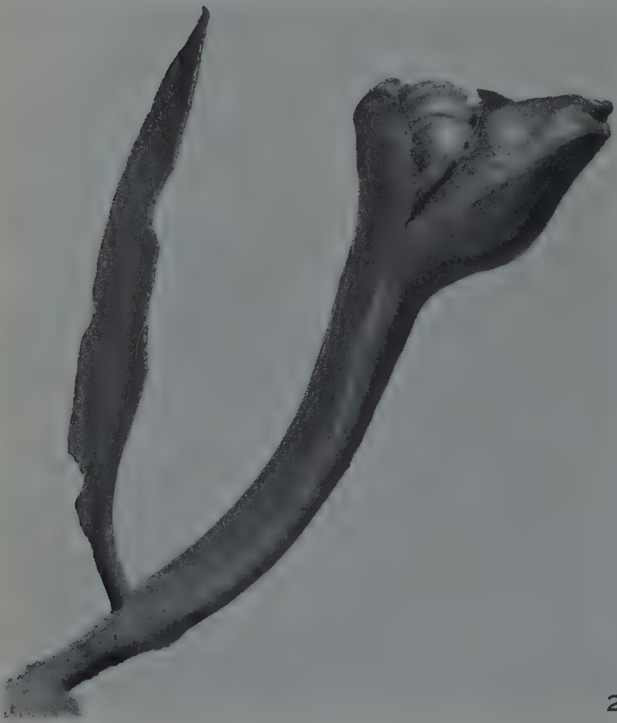

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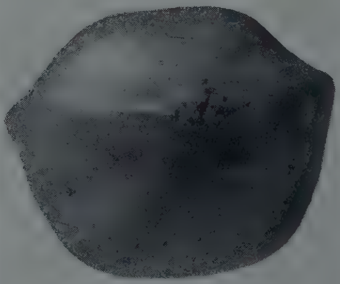

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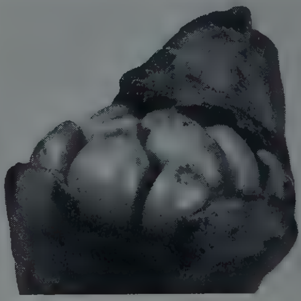

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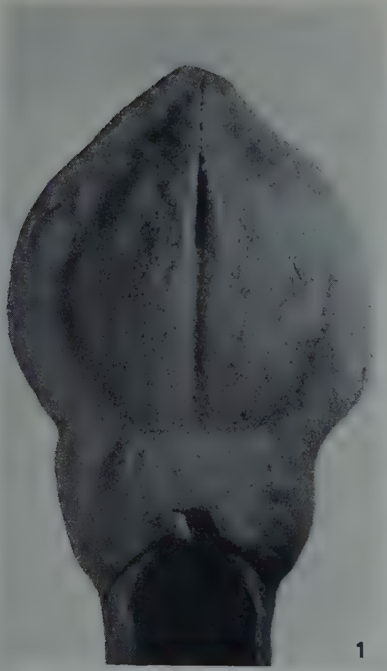

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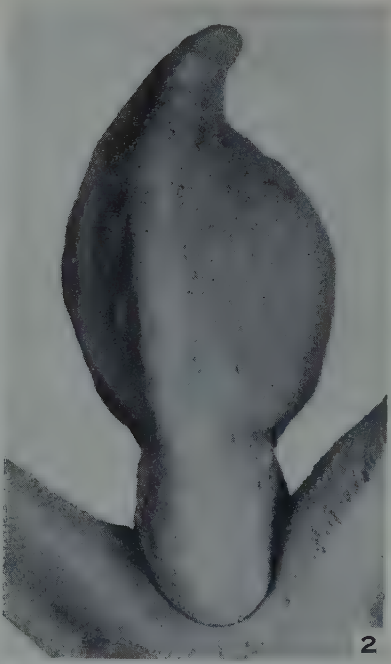

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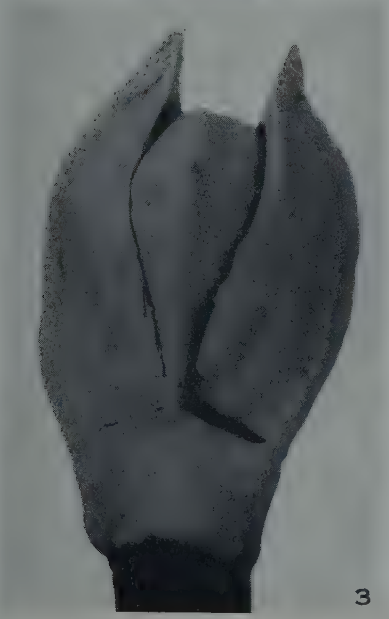

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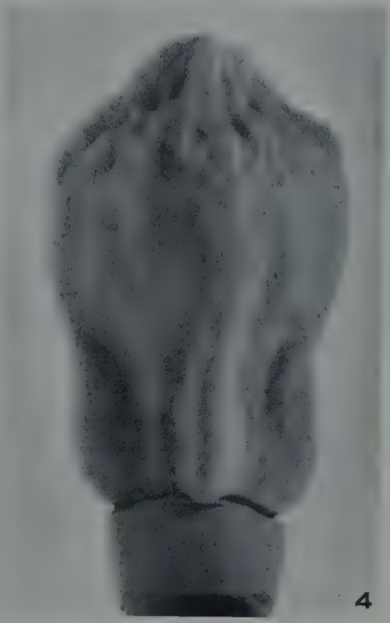

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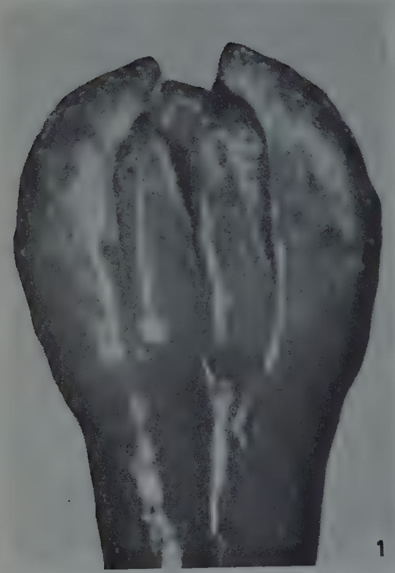
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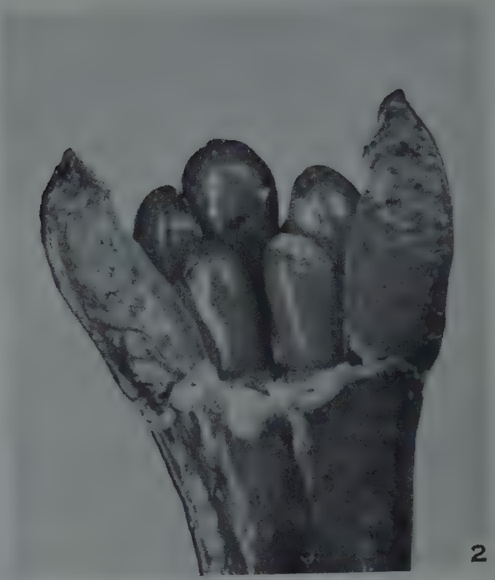
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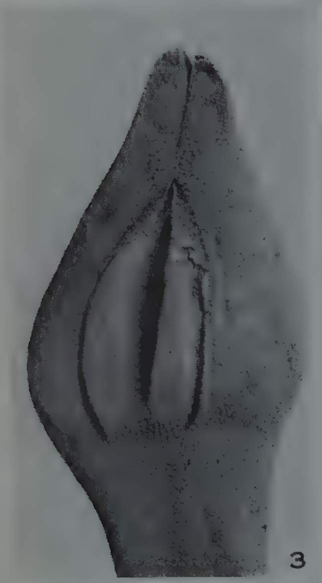
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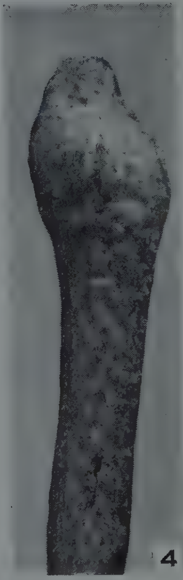
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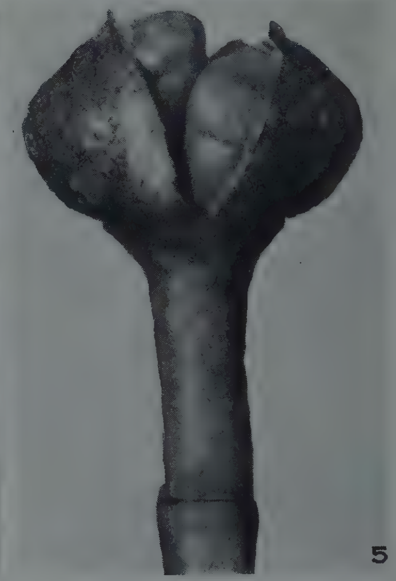
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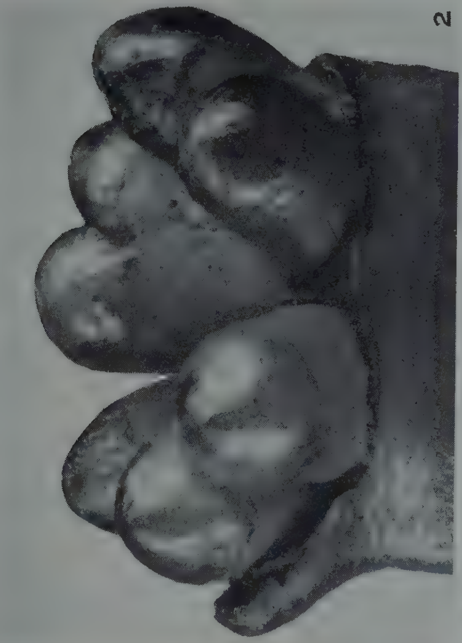

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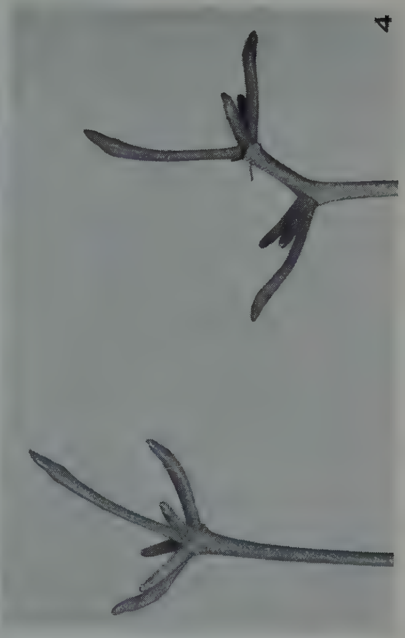

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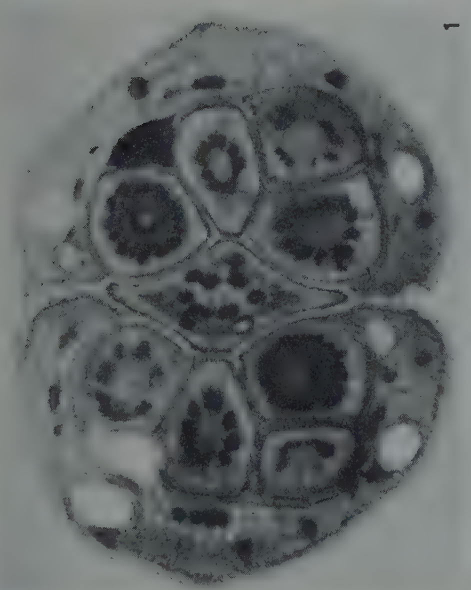

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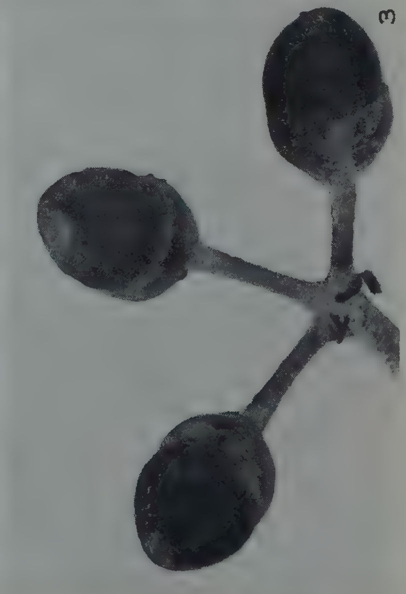

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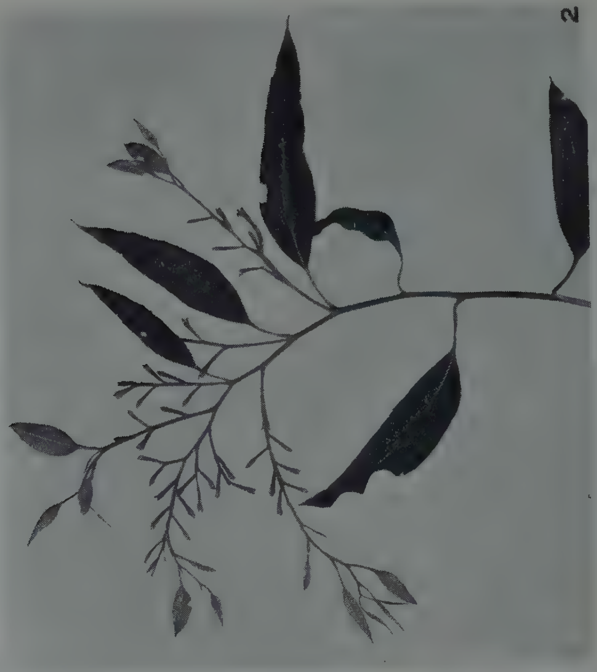
MORPHOLOGY OF FLORAL ORGANS OF EUCALYPTUS. I



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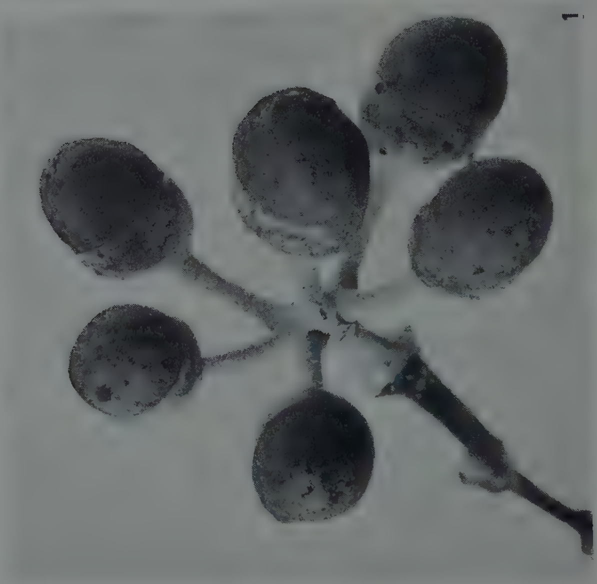

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APPENDIX I

Structure of Unit Inflorescences of Species of Eucalyptus

The information contained in the following table was obtained from dissections of inflorescences of fresh or herbarium material. In a few cases, only a few buds have been examined, but in most cases at least six, and as many as a hundred, have been dissected.

The species names are those adopted by Blakely (1955), who gives the authorities and synonymy. Information on some of the species listed in the table is given in the text.

The number of flower buds in the clusters may vary, both on the same tree and in different trees of the same species. The specimens we have been able to examine (e.g. *E. maideni*) may not always illustrate either the normal flower number or its full possible range.

The bracts constituting the involucre are referred to their successive series beginning with series 2 (the Deckblatt constituting series 1). Each series is separated by a colon from the next. Brackets indicate fusion of the bracts, e.g. (2) indicates two fused bracts, and (2 : 2 + 2) indicates that the two bracts of series 2 and the four of series 3 are all fused together. In series 3, the first number indicates the anterior pair and the second number the posterior pair of bracts. Thus, 2 : 2 + (2) indicates that all the bracts, except the posterior pair of series 3, are free. In series 4 and beyond, the pairs of bracts indicated by 2 + 2 are in all instances external to the flower cluster. In one or two cases, the internal members of series 4 are developed as well, and this is indicated as 4 + 4.

Species	Number of Flower Buds in Unit Inflorescence	Constitution of Involucre
alpina	3, 7	2 : 2 + 2
baxteri	15	2 : 2 + 2
beyeri	3, 7	2 : 2 + 2
	7	2 : 2 + 2 : 2 + 2
bicolor	3	2
	4	2 : 2 + 2
	7	2 : 2 + 2
bicostata	3	2
	3	2 : 2 + 2
botryoides	7	(2 : 2 + 2)
caesia	3	2
calophylla	7	2 : 2 + 2 : 2 + 2
		2 : 2 + 2 : 4 + 4 (10–14 free bracts)
cambageana	7	2 : 2 + 2 : 2 + 2
cephalocarpa	7	(2 : 2 + 2)
cinerea	3	2
citriodora	3	(2) : 2 + 2

Species	Number of Flower Buds in Unit Inflorescence	Constitution of Involucre
cladocalyx	11	2 : 2 + 2 : 2 + 2 : 2 + 2
consideniana	7–11	(2 : 2 + 2)
**cornuta*	15	(2 : 2 + 2) : (2 + 2 : 2 + 2)
	19	2 : (2) + (2) : 2 + 2 (young inflorescence buds)
dives	19–23	(2 : 2 + 2)
elaeophora	7	(2 : 2 + 2)
foelscheana F. Muell	7	2 : 2 + 2
ficifolia	7	2 : 2 + 2 : 2 + 2
		2 : 2 + 2 : 4 + 4 (10–14 free bracts)
gigantea	11	(2 : 2 + 2)
globulus	1	2
	3	2
gomphocephala	7	2 : 2 + 2
hemiphloia	7	2 : 2 + 2 : 2 + 2
incrassata	7	2 : 2 + 2 : 2 + 2
kitsoniana	2–7	(2 : 2 + 2)
kybeanensis	7	(2 : 2 + 2)
latifolia	3	2 : 2 + 2
**lehmanni*	15	[(2 : 2 + 2) : (2 + 2 : 2 + 2)]
	19	(2 : 2 + 2) : (2–10 in inner whorls) (younger inflorescences)
leucoxylon	3	2
macarthuri	3	2
macrorrhyncha	7	2 : 2 + (2) (posterior pair often fused to series 2 bracts)
maculata	3	(2) : 2 + 2
maideni	3	2 : 2 + 2
miniata	9	(2 : 2 + 2)
mitchelliana	11	(2 : 2 + 2)
**nutans*	7	2 : 2 + 2
obliqua		
(Lysterfield, Victoria)	11	(2 : 2 + 2)
(Waterloo Bay, Victoria)	7	(2 : 2 + 2)
odontocarpa	3	2
oleosa	7	2 : 2 + 2
	9	2 : 2 + 2 : 2 + 0
ovata	7	(2 : 2 + 2) : 2 + 2 (1 to 4 free bracts in inner whorl)
pachyloma	7	2 : 2 + 2
pallidifolia	7	2 : 2 + 2 : 2 + 2 (1 to 4 free bracts in inner whorl)
paniculata	7	2 : 2 + 2 : 2 + 2
	7	2 : 2 + 2
pauciflora	11, 15, 19	(2 : 2 + 2)
(coppice shoots)	33, 43, 47, >60	(2 : 2 + 2)

Species	Number of Flower Buds in Unit Inflorescence	Constitution of Involucre
phoenicea	18, 22	(2 : 2 + 2)
pilularis	11–15	(2 : 2 + 2)
**platypus*	7	2 : 2 + 2
preissiana	3	2
pulverulenta	3	2
radiata	11, 15, 19, 23, 37	(2 : 2 + 2)
regnans	7–15	(2 : 2 + 2)
risdoni	9, 11, 13	(2 : 2 + 2)
robertsoni	11	(2 : 2 + 2)
robusta	7	(2 : 2 + 2)
rudis	7	2 : 2 + 2 : 2 + 2
saligna	7–11	(2 : 2 + 2) : 2 + 2 (1–4 bracts in inner whorl)
	7	(2 : 2 + 2)
sepulcralis	7–11	(2 : 2 + 2)
sideroxylon	3	2
	7	2 : 2 + 2 : 2 + 2
	9	2 : 2 + (2) : 4 + 4
sieberiana	7–15	(2 : 2 + 2)
smithii	7	(2 : 2 + 2)
stellulata	11, 13, 15	(2 : 2 + 2)
stellulata var.†	11	(2 : 2 + 2)
stricta	7	(2 : 2 + 2)
tetragona	3	2
tetrodonta	3	2
todtiana	7	2 : 2 + 2
torquata	7	2 : 2 + 2
	7	2 : 2 + 2 : 2 + 2
	6	2 : 2 + 1
transcontinentalis	7	2 : 2 + 2
viminalis	3	(2)
vitrea	7	(2 : 2 + 2)
**wandoo*	7	2 : 2 + 2 : 2 + 2

* In the Cornutae the bracts appear to be free in many species in the smaller inflorescences, but at maturity, owing to the great enlargement of the bases of the bracts which may have taken place, they appear to be fused except at their tips. Thus, in *cornuta* and *lehmanni*, inflorescence buds with involucre *circa* 5 mm long have at least some of the inner bracts free. In *nutans*, only the most basal parts of the bracts are fused.

† = *macrorrhyncha* var. *nana*.

THE STRATIGRAPHY AND HISTORY OF GROENVLEI, A SOUTH AFRICAN COASTAL FEN*

By A. R. H. Martin†

[*Manuscript received April* 9, 1959]

Summary

Borings on the fen at Groenvlei show that the earliest sediment was a diatomaceous nekron mud in a small freshwater lake. This filled in and fen peat formed over it. Subsequently, marine mud was spread over almost the whole basin, the course of the transgression being followed by diatom analysis. A change in composition of the marine diatom flora, apparently due to an unexplained change of temperature of the sea, is recorded.

The marine incursion graded into brackish lagoon stages, towards the end of which conditions were rather unfavourable to diatom growth, followed by increasingly freshwater conditions, during which calcareous muds were laid down. The eastern basin of the lake became more or less separated from the main lake by a sand bar. The calcareous lake mud was overgrown by the latest reedswamp and sedge fen.

Radiocarbon dating gave an age of 6870 years for a sample from the upper part of the submerged peat bed at Groenvlei, and a lapse of little under 5000 years before freshwater deposits again occupied the eastern basin of the lake (^{14}C age of gyttja sample, 1905 years).

This dating of the Groenvlei transgression is compatible both with the main post-Glacial eustatic rise of sea-level in the North Temperate latitudes, and with similar transgressions on the coasts of south-eastern Australia, New Zealand, and Fuego-Patagonia. The maximum height of the sea-level is considered to have been about 1·5 m higher than at present.

I. Introduction

The Knysna-Wilderness lakes of South Africa, of which Groenvlei is one, lie on the south coast of the Cape Province in a narrow coastal belt, behind which a line of coastal mountains rising to about 1200 m (4000 ft) at distances of 13–32 km inland, ensure a fairly high and uniform rainfall (700–1300 mm per annum). Unfortunately few studies of lake sediments have been made in South Africa. Hutchinson, Pickford, and Schuurman (1932) considered that most South African lakes were shallow and impermanent, and it does appear that the sediments of many lakes are liable to be periodically exposed and subjected to oxidation and deflation by wind erosion, thus obscuring the record. It was therefore of great interest to find below the fen peat at Groenvlei a not inconsiderable depth of sediment apparently laid down continuously over a long period and containing abundant organic remains, including molluscs, Foraminifera, ostracods and other Crustacea, diatoms, oospores of Characeae, and remains of higher plants, including pollen.

At Ruigtevlei, where a somewhat parallel series of sediments has been laid down, conditions were evidently much less favourable for the preservation of remains.

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*Some of the work reported in this paper forms part of a thesis approved in 1955 for the degree of Doctor of Philosophy in the University of London.

†Botany School, University of Sydney.

The present paper describes the Groenvlei stratigraphy, with special reference to the evidence of subfossil diatoms. The implications of this evidence in terms of lake history during the Holocene are briefly examined. The evidence of pollen analysis will be considered in a further contribution.

II. The Stratigraphy of the East Fen

The deeper sediments at Groenvlei underlie the east fen, described elsewhere (Martin, in press). Along the north shore of the lake the peat is only 60–100 cm deep, lying on a sandy shelf. The profile of the south shore is so steep that no fen deposits have formed. At the western and south-western end, the peat is only a few centimetres to 50 cm deep over sand and thin calcareous muds. The south-east saltmarsh has *c*. 4 m of sediments which are continuous with those of the east fen.

A considerable depth of sediment undoubtedly exists on the lake floor. One boring made from a boat in 3 m of water penetrated 1·6 m of homogeneous lake mud without reaching any different type of sediment; with the light Hiller-type borer available such sampling proved very difficult.

Since the part of the fen which superficial inspection suggests might be the deepest is in fact mainly underlain at 1–2 m depth by sand, the filled-in lake basin was only revealed when several lines of probes were made transversely across the fen with a soil auger to find the bottom contours (Fig. 1). Subsequently more detailed studies were made along selected transects.

The superficial fen peat, consisting mainly of *Cladium* roots and rhizomes, was found to be underlain by a bar of sand varying from clean and white to brown and muddy, and containing shell layers. This bar thins out close to the lake, being represented only by a thin sandy shell layer. Below the greater part of the fen meadow the sand is thick, but thins out again further from the lake and is absent altogether beyond 450 m east of the lake (Figs. 1, 4). The surface of the bar is slightly convex in transverse section, the crest being just below present lake level. Wedges of calcareous lake mud lie between it and the peat at its margins and the bar itself lies on marine mud. Its origin may be due to wave and current action produced by westerly winds at the head of the lake. At the northern side, wind-blown sand has been piled onto the bar, so that it rises above the peat level as a sand ridge. It passes laterally into the north shore sand platform. Where the sand is absent, the peat lies on more or less calcareous creamy white or brownish organic lake mud, containing layers of freshwater shells, mostly of *Burnupia capensis*, *Succinea* sp., and *Bulinus tropicus*. *Chara* oospores and *Cladium* fruits are the commonest identifiable macroscopic remains. Passing downwards, the mud becomes firmer and more silty, though still calcareous, and in consistency and colour resembles soft putty. In this mud, Foraminifera begin to be recorded at a depth of from 2·4 to 3 m in different boreholes, while shells of small brackish-water gasteropods (*Tomichia* sp.) and mussels (*Modiola capensis*) form a distinct layer varying from about 3 to 3·5 m in depth. Below this, Foraminifera and molluscs, now including *Dosinia* sp. and *Nassarius kraussianus*, are more frequent, the mud now being grey-black (greenish closer to the present lake), firm, and rather silty. At 3·8–5·7 m black amorphous peat is struck, nearly the same colour as the mud immediately

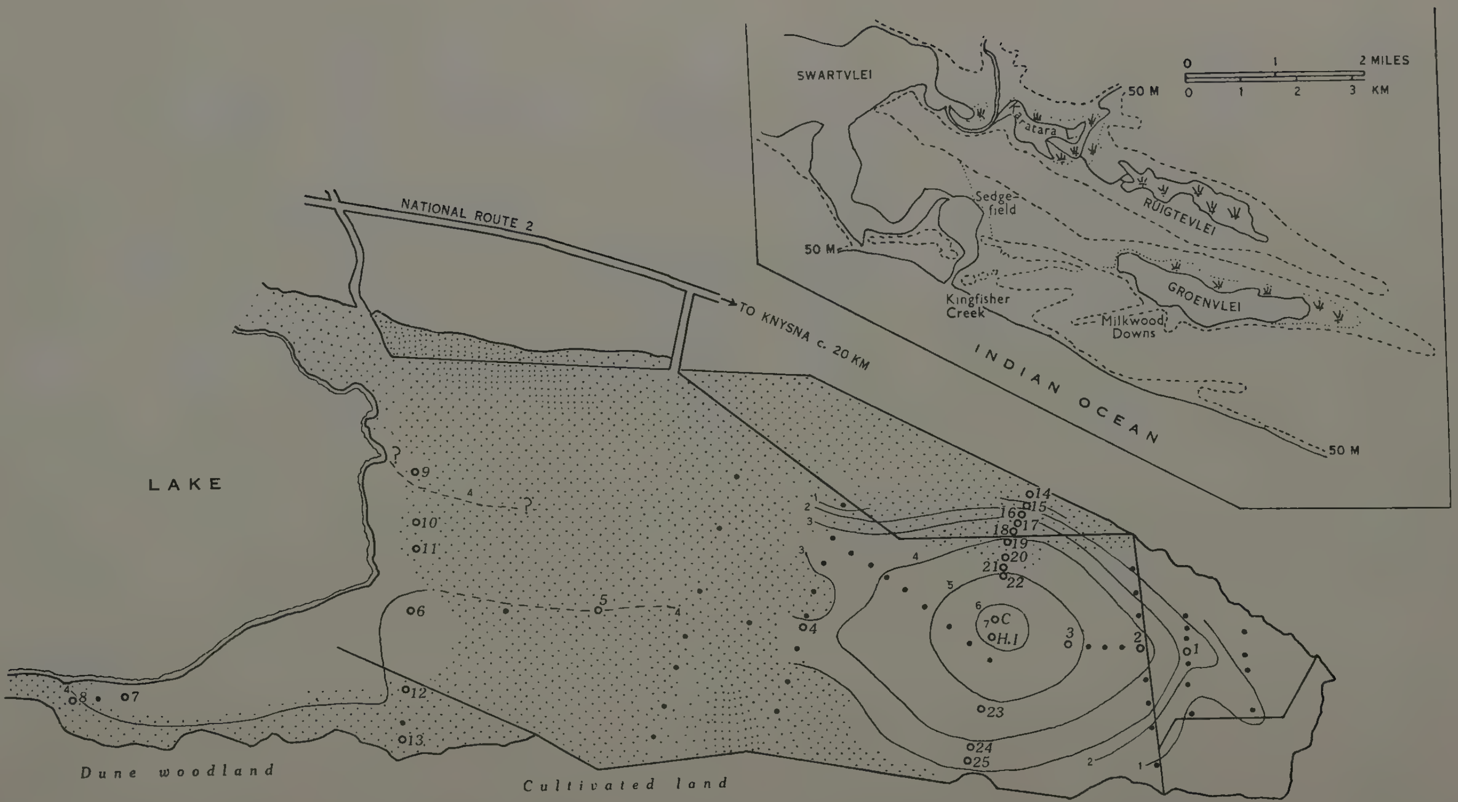
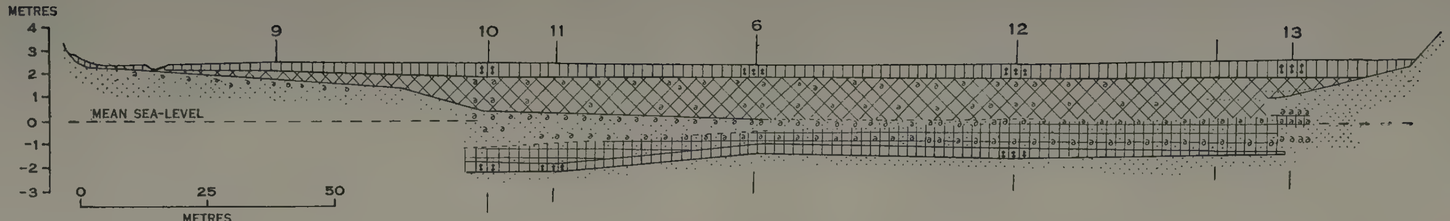
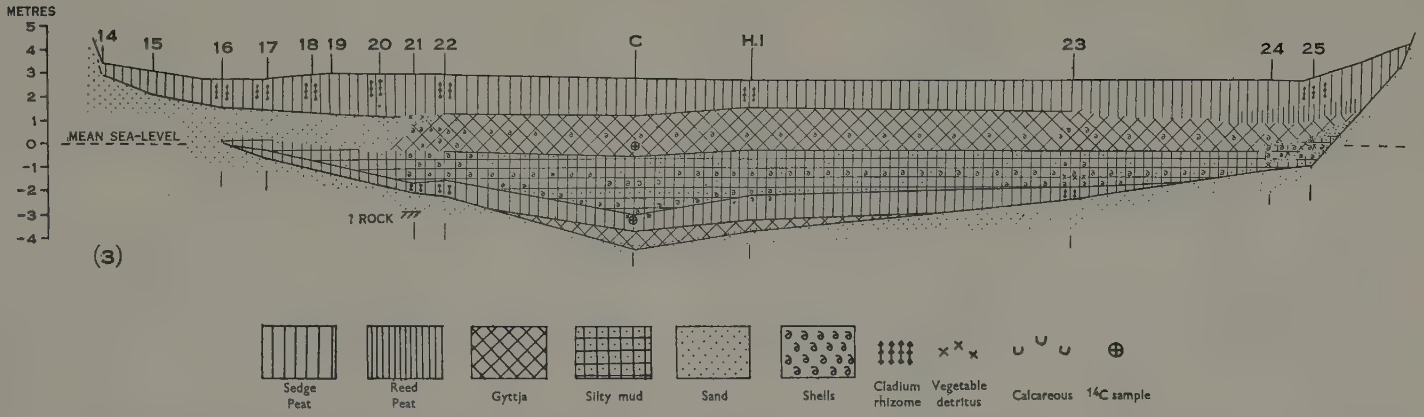

SWARTVLEI
0 1 2 MILES
0 1 2 3 KM
50 M
atara
Sedge field
RUIGTEVLEI
50 M
GROENVLEI
Kingfisher Creek
Milkwood Downs
INDIAN OCEAN
50 M
NATIONAL ROUTE 2
TO KNYSNA c. 20 KM
LAKE
Dune woodland
Cultivated land
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
C
H.I
?

Fig. 1.—Map of the positions of the borings on the east fen, showing contours of the fen basin. O Numbered borings from which complete stratigraphic record was obtained. ● Auxiliary borings from which only partial records were obtained. *H.I*, position of diatom analysis core. *C*, position of ^{14}C core. Inset: country between Groenvlei and Swartvlei; land above 50 metres shown by formline.


METRES
4
3
2
1
0
-1
-2
-3
MEAN SEA-LEVEL
9
10
11
6
12
13
0
25
50
METRES

(2)


METRES
5
4
3
2
1
0
-1
-2
-3
-4
MEAN SEA-LEVEL
14
15
16
17
18
19
20
21
22
C
H.1
23
24
25
? ROCK
Sedge Peat
Reed Peat
Gyttja
Silty mud
Sand
Shells
Cladium rhizome
Vegetable detritus
Calcareous
14C sample

(3)

Fig. 2.—Transverse profile of the lake deposits, c. 35 m east of the lake margin, showing thin spread of sand across the basin at 2 m depth.

Fig. 3.—Transverse profile of the lake deposits c. 670 m east of the lake margin, showing positions of ^{14}C samples and main pollen and diatom cores.

above it, but cheesy or friable and with very little sand or other inclusions except a few shells near the top, usually fragmentary. The peat bed varies from a few centimetres thick marginally to *c.* 70 cm in the centre, where it is underlain by non-calcareous brown nekron mud rich in diatoms and slightly sandy, especially in the last few centimetres.

The floor of the basin is of sand, usually coarse and white in the centre, in places almost milky owing to a percentage of fine white silt, or brownish and humus-stained from the overlying peat, but never muddy. It was penetrated to a depth of about a metre in a few borings but was homogeneous and nearly sterile, only a single lamellibranch shell being recovered from it. Whether this sand was water- or wind-deposited could not be determined, though the presence of fine silt and apparently also shells, although very sparse, suggests the former. In hole No. 21 the borer struck hard solid material which may have been calcified sand rock. The deepest part of this basin is slightly towards the northern side, forming an apparent trough, 4·0–7·0 m in depth.

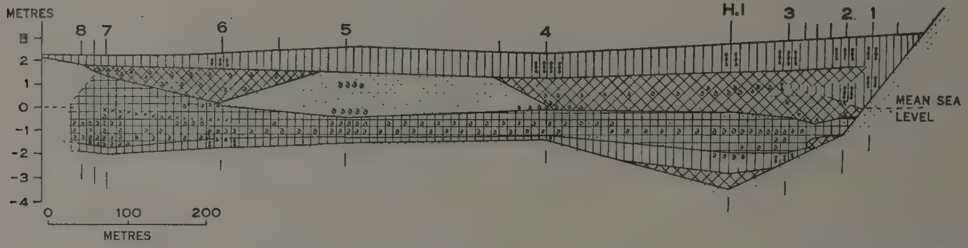


Fig. 4.—Longitudinal profile of the filled-in basin of upper Groenvlei below the east and south-east fens. The left-hand side of the diagram is an oblique section of the deposits below the south-east fen. The sand bar rests on marine-brackish muds. For explanation of symbols used, see key to Figs. 2 and 3.

In several borings, mostly close to the southern margin, the lower peat, here only about 10–14 cm thick, contained a bed of white sand 1–2 cm thick, a little above the basal sand. The scale of Figures 2–4 is too small to show the details, and these figures are further simplified by the omission of symbols distinguishing calcareous from non-calcareous muds.

The chief features of the three sections are the grey-brown, black, and greenish silty foraminiferal-shell muds, which clearly indicate marine influence, immediately overlying basal peat and freshwater deposits; and the spread of sand over these muds from both shores, but chiefly from the north, separating the small eastern basin from the long main basin of the lake. The topmost deposits represent stages of the filling in of an essentially freshwater lakelet and the formation of a sedge fen. Borings Nos. 6, 7, and 8 on the longitudinal section, which is deflected onto the south-east fen and saltmarsh, show that this bay of the main lake has filled up in much the same way as the east fen, silty mud being thicker, however, in borings 7 and 8.

A preliminary report on the Foraminifera and other microscopic animal remains from boring H.I appears as Appendix I. The lower part of the foraminiferal mud (from *c.* 520 cm in H.I) must have been laid down in marine or near-marine conditions, the upper part from 390 to *c.* 300 cm in more brackish conditions, possibly fluctuating in salinity. Foraminifera die out at about 300 cm but a very small number were found at 160 cm. These do not appear to be reworked, and sampling contamination is in this instance out of the question, but their presence in apparently fresh-water mud is possibly due to accidental introduction during treatment, as examination of a fresh sample at this level revealed no more and no corresponding fluctuation in diatoms occurred at this level.

The diatoms give more precise information about the salinity conditions, and support the division of the mud into a lower marine and upper brackish section. They are discussed in detail below.

Between borings Nos. 3 and 2 in the longitudinal section the marine muds appear to pass laterally into brackish. Samples for diatom analysis were not kept but the sequence is fairly clear from the boring logs. In boring No. 3, grey-brown foraminiferal muds occur from 336 to 371 cm; at 371 cm *Tomichia* and *Modiola* occur, and from here to 484 cm where the lower peat begins, the mud is grey to black, with Foraminifera and shells, the last few centimetres above the peat being very black and less silty. In the nearest auxiliary boring to No. 3 the shell layer occurs at 374 cm; and the grey-brown mud above it only commences at 345 cm. The sediment from 374 to 450 cm, where peat commences, is similar to that in No. 3 but shells are absent in the last 30 cm. In the next boring coarse and fine detritus gyttjas occur down to 369 cm; a few pieces of rhizome were found at this depth. Below 369 cm grey cohesive foraminiferal mud with no shells occurred down to *c.* 412 cm. These clearly correspond with the marine muds, but from 412 to 458 cm less silty and non-foraminiferal black organic mud occurs before peat is struck. This appears to be homologous with the narrow black transitional zone between the marine mud and peat in the previous borings. The peat here is only 3·5 cm thick. In the next boring gyttja occurs to *c.* 367 cm; below this occurs some 60 cm of soft fine-grained light-brown to chocolate-coloured mud before the basal sand is struck; the peat has died out. In boring No. 2, gyttja occurs to *c.* 330 cm, soft grey-brown wet sandy mud which tended to run off the auger from 330 to 365 cm, soft pale brown and chocolate mud from 365 to 382 cm, then basal sand. The last few centimetres of chocolate mud contained a few seeds. These terracotta- or chocolate-coloured muds were recorded at about the same depth (3·5–4 m) all round the margin of the basin, were devoid of Foraminifera and shells, and were not rich in diatoms, but contained small quantities of *Botryococcus* which was not detected in other types of sediment. The marginal location suggests inwash of much-weathered material containing little organic matter, such as could be derived from the erosion of red ferruginous layers which occur in the dunes. Alternatively, some oxidation of marginal sediments may have occurred during a temporary low lake level.

Minute crystals of black ferric sulphide occur in the marine and more brackish muds from about 3 m downwards, often forming inside pollen grains and other microscopic structures and rendering them too opaque for identification. Twenhofel (1950) considers the development of sulphide to be favoured by salt water and poor circulation as in a lagoon with little or no tide, conditions which undoubtedly apply here.

A line of borings across Ruigtevlei at about its widest and deepest point struck sand at depths of 0·7–2 m. The peat is generally more humified than that at Groenvlei and few remains could be identified. At the base there are, in some borings, a few centimetres of coarse detritus or calcareous lake mud or both, mostly towards the northern side. Ruigtevlei appears to have always been much shallower than Groenvlei and terrestrial peat forms by far the greater part of the organic deposits.

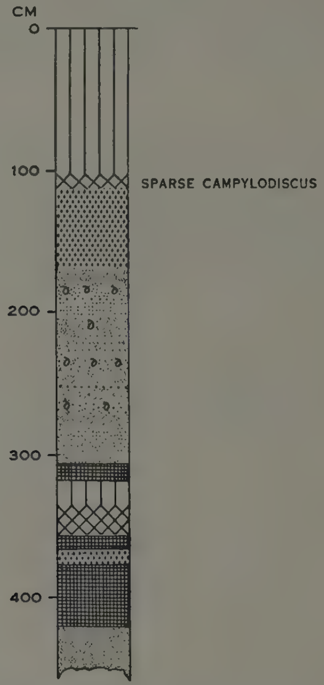


Fig. 5.—Stratigraphic sequence in boring R.II at Ruigtevlei: the only point at which the stiff silt and clay separating the upper and lower peats was penetrated. The material from 160 to 300 cm had to be removed with a soil auger, consequently boundaries in the sediment were more difficult to make out.

In the lower basin of Ruigtevlei, at a depth corresponding to the sand in the upper basin, a tenacious white clay was found. This suggested that the sand might correspond to it and have been laid down under aquatic conditions. Accordingly, several attempts to penetrate the sand were made, only one of which was successful. The lowermost deposit (Fig. 5) is a sandy-clay mud, on which lies half a metre of black amorphous silty-clay mud. At about 360 cm this changes to nekron mud, but peat formation soon began, and the peat merges into more black clay mud. Then follows a considerable depth of coarse and fine silty-clay mud with shells, culminating in over half a metre of muddy sand before the deposits of the freshwater lake (containing a sparse diatom flora including *Campylodiscus*; see Section III) and the upper peat are recorded. Diatoms could not be detected throughout most of the profile, but siliceous sponge spicules were abundant at some levels. None the less, the similarity to the Groenvlei sequence is striking, and as the lakes are at very similar levels, it must be supposed that the silty-clay muds separating the upper and lower freshwater deposits at Ruigtevlei represent the expression of the marine transgression in a site further from the sea.

III. The Diatom Succession

(*a*) *Methods*

The treatment of diatom samples is described in Appendix II. Counts of diatoms cannot be based on equivalent percentage values for all species, as local bursts of minute colonial epiphytes make the results meaningless. A basic sum was therefore chosen, consisting of all the identifiable species larger than 40 by 7 μ in linear dimensions, valve view. These represent in the main the "dominant" benthic, tychoplanktonic, and epiphytic forms. A fairly stable composition was obtained, none of the species being subject to sudden bursts of great abundance. This is essentially the density method of Budde (1942), but adapted to usage more like that of pollen analysis (see also Jørgensen 1948).

The only serious deficiency in this method arises with *Melosira sulcata*, which, being circular in section, is of greater volume than some of the diatoms included in the 100 per cent. sum. As this is the commonest species present at some levels, its exclusion, though justifiable, might lead to a spurious increase in the number of traverses required to obtain the 100 per cent sum. So long as this is borne in mind, no difficulty need arise. The larger diatoms have been classified as far as possible in halobion spectra (Fig. 6) and pH spectra, under the ecological groupings of Kolbe (1927), Boye-Petersen (1943), Jørgensen (1948), and others. The smaller diatoms (Fig. 7) are arranged in systematic order, as the grouping of all of these into spectra was not feasible. Temperature classification appears to be too unreliable except in so far as the marine "temperate" and "tropical" forms have a temperature implication rather than a purely geographical one.

(*b*) *Results*

Samples were analysed at intervals of 5–30 cm in boring H.I. The layers recognized have been identified by symbols, which appear on the right-hand side of Figures 6–8.

At 630 cm, which is just on the boundary between the basal sand and the organic lake mud (F1), and consequently has a low loss on ignition, the flora consists mainly of *Cymbella cymbiformis*, *C. mülleri*, *Fragilaria pinnata*, *Gomphonema gracile*, and *G.* cf. *parvulum*. *Synedra acus* and *S. ulna*, *Anomoeoneis sphaerophora*, *Navicula radiosa*, *Epithemia zebra*, and a few others are also present. Halophiles and mesohalobes are few, *Cocconeis clandestina*, *Mastogloia elliptica* var. *dansei*, *N. peregrina*, and *Campylodiscus clypeus* being the commonest. The general impression is one of a small freshwater lake slightly influenced by proximity to the sea, and about neutral in reaction. No alkalibionts are abundant, and the presence in small quantities of

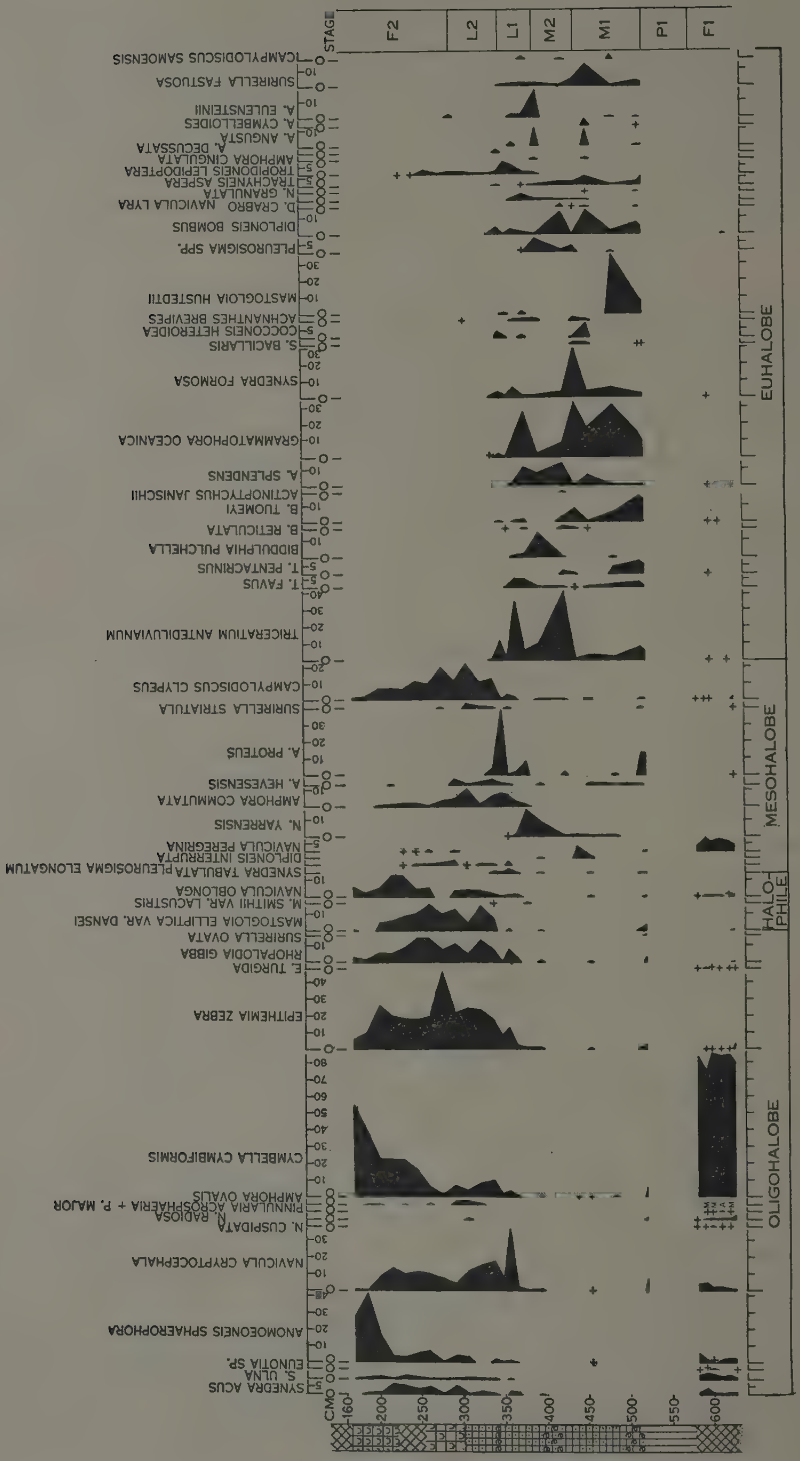


Fig. 6.—Diatom analysis of boring H.I, large species only. For explanation of symbols used for sedimentary columns of Figs. 6 and 8, see key to Figs. 2 and 3.

acidophiles such as *Eunotia* and *Pinnularia* spp. makes it unlikely that the lake was highly alkaline. *Chara* oospores are absent and the carbonate content is nil.

This assemblage remains very constant throughout the existence of the lake. Mesohalobes, other than *Navicula peregrina*, become very unimportant; *Epithemia turgida* replaces *E. zebra*; *Navicula cuspidata* enters the flora; *Gomphonema gracile* and *Fragilaria pinnata* become commoner. Marine diatoms, often fragmentary, are present in very small quantities. It is not possible to decide whether they represent sampling contaminants or normal inwash, but they appear quite alien to the general facies of the flora.

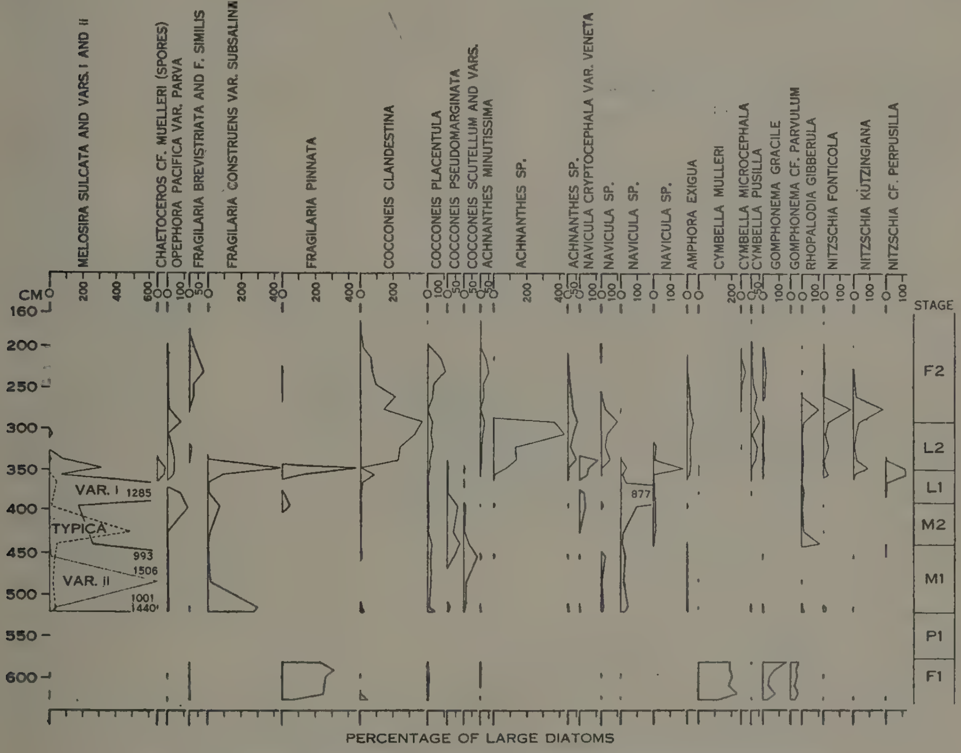


Fig. 7.—Diatom analysis of boring H.I, the commoner smaller species.

The lower peat (P1), in which *Cladium*, *Cyperus*, and *Thelypteris* seem to have been most important (i.e. a Macrocaricetum-Filicales peat), is almost devoid of diatoms, the number of traverses required for a count of 150 being about 1000 (estimated). Consequently no complete counts were made. At about 521 cm the number of diatoms sharply increases, nearly all being marine forms. At the same time, loss on ignition falls from *c.* 90 to *c.* 45 per cent. and carbonate, mainly in the form of shells and Foraminifera, increases to about 40 per cent. At 516 cm the freshwater forms have nearly all dropped out and an almost purely marine assemblage of species occurs. Loss on ignition continues to drop to *c.* 25 per cent. The sediment is now the grey-black silty foraminiferal-shell mud (M1 and M2).

The main feature of the marine flora is the sharp change in its composition at *c.* 440 cm. The more abundant species above this level (M2) are mainly temperate forms of wide temperature tolerance, e.g. *Actinoptychus splendens*, or else definite cool temperate forms, scarcer in warmer water, e.g. *Triceratium antediluvianum* (which temporarily assumes dominance) and *Biddulphia pulchella*, while most of the diatoms which become rare above this boundary are definite warm temperate and tropical ones, e.g. *Triceratium pentacrinus*, *Biddulphia tuomeyi*, *Synedra bacillaris*, *S. formosa*, *Cocconeis heteroidea*, and *Mastogloia hustedtii*. *Grammatophora oceanica* and *Melosira sulcata*, which decrease and recover again, are more cosmopolitan forms. *Surirella fastuosa* is one of the few apparently cosmopolitan species commoner below the boundary, while *Triceratium favus* is interesting in being represented mostly by triangular forms in the upper part and quadrate forms in the lower part of the marine section. Mr. R. Ross allows me to quote his opinion that this may also indicate a temperature distinction.

Such a change in flora might be due to a change in the system of currents, which enabled colder water to come along the coast, or possibly to general ocean cooling. The change was perhaps temporary, for it will be noticed that at about 370 cm *Mastogloia hustedtii*, *Biddulphia tuomeyi*, and *Synedra formosa* show some signs of recovery, and in boring No. 11 on the seaward side of the sand bar, *Triceratium pentacrinus* was found as high as 220 cm. So little is known of either the distribution of the modern diatom flora of the South African littoral zone, or the variations in ocean currents, that no explanation of this apparently long-term fluctuation can be offered. It is well known that cold "Antarctic" water may well up off the South African coast periodically, causing death or numbing of fish shoals, but these are minor fluctuations lasting only a few days. An actual fall in the mean temperature of the warm Agulhas current, which normally bathes this coast, must have been involved here. A mere ecological effect due, say, to a change in circulation in the embayment seems improbable, since under the prevailing conditions such a change would more likely be expressed by a change in the ratio of euhalobic to mesohalobic forms. Records of palaeotemperature changes in sea-water (Emiliani 1955, 1958) suggest a lowering of temperature of the surface water of the open sea by about 1 to 1·5°C within the last 5000 years, but it would be premature to link this with the fluctuation reported here. Such analyses refer mainly to North Tropical water of the Atlantic and to pelagic Foraminifera. The diatoms in the present investigation are littoral forms in a slightly extratropical region of the Indian Ocean.

Above 390 cm, brackish and freshwater species again enter the profile. In particular, *Navicula yarrensis* has a peak at 378 cm, *N. cryptocephala* at 356 cm (surprisingly, as it is not usually considered a brackish species), and *Amphora proteus* at 348 cm. *Fragilaria construens* var. *subsalina* and *F. pinnata* (var.?) are also very abundant at about this level, and *Navicula cryptocephala* var. *veneta* (or aff.) is common a little below the level at which *N. cryptocephala* (*typica*) has its peak. An unidentified *Navicula*, presumably a mesohalobe, reaches 877 per cent. at 378 cm. There is evidence in these sudden fluctuations that the salinity was varying considerably between 390 and 340 cm, the level at which marine species died out.

The behaviour of *Tropidoneis lepidoptera*, a supposedly marine form, is anomalous. It stands out clearly as a mesohalobe. Prof. H. Giffen (personal communication) finds that this species today is a typical form of brackish lagoons near East London, together with *Navicula yarrensis*. The maxima of these two do not quite coincide in the profile, *Tropidoneis* reaching a maximum a little later than *Navicula yarrensis*. From 378 to 356 cm, however, both are common together. This may be called lagoon stage 1 (L1).

Florin (1946) has suggested that a definite lagoon flora dominated by *Campylodiscus clypeus*, *Amphora mexicana*, *Surirella striatula*, *Nitzschia scalaris*, and others occurs in Swedish marine-invaded profiles during the brackish phase. While *Campylodiscus clypeus* is common in this South African profile and, owing to its large size, appears in some uncleaned samples to dominate the flora, it does not have a very definite associated flora which could be named a "*Clypeus* lagoon flora". During much of the period in which it is relatively one of the commonest diatoms it is in absolute terms rather scarce, as between 340 and 290 cm all diatoms are much reduced in numbers (Fig. 8). Between these levels, *Cocconeis clandestina* and *Achnanthes* sp. (probably undescribed) are numerically the commonest diatoms. *Amphora commutata*, *A. hevesensis*, *Surirella striatula*, and *Nitzschia scalaris* (not plotted in Fig. 6 since it was represented only by a few fragments) are fairly constant, though by no means numerically abundant, associates at this level. These, if anything, represent the "*Clypeus* lagoon flora", but at this stage the lake appears to have been somewhat unsuitable for diatom growth. *Tropidoneis* persists through this stage, which may be called lagoon stage 2 (L2). These two stages are not proposed

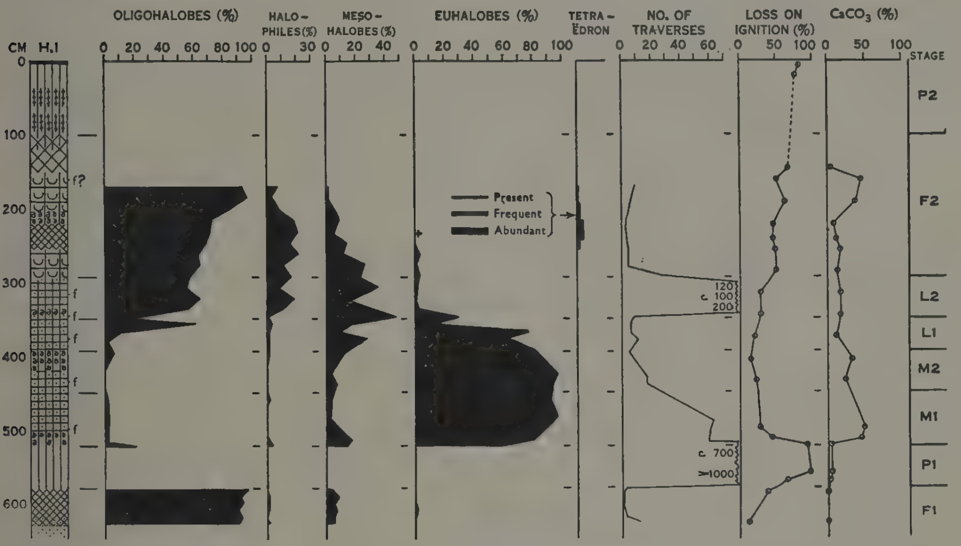


Fig. 8.—Distribution of halobion classes of diatoms in boring H.I. On the right: number of traverses required to obtain 150-diatom sum from equal volumes of sediment. *f*, Foraminifera samples.

in any general sense, but purely as descriptive terms for this particular lake, stage 2 being less saline than stage 1.

Above 292 cm the nature of the lake changed rapidly (F2), *Epithemia zebra*, *Rhopalodia gibba*, *Mastogloia elliptica* var. *dansei*, and *Campylodiscus clypeus* all being abundant. The lake mud is calcareous, this now being due to non-structural calcium carbonate rather than to Foraminifera and shells as lower down. At *c.* 250–220 cm there is a band of brown mud of lower carbonate content. This is the level at which *Cymbella cymbiformis* once more assumes importance and *Campylodiscus* begins to decline. *Navicula oblonga* and *Mastogloia elliptica* var. *dansei* here reach their highest frequencies and thereafter decline; *Cocconeis placentula* passes in abundance the more brackish *C. clandestina*. Above 220 cm there is a shell layer (mainly *Burnupia*), then shelly, very calcareous mud, calcium carbonate rising to 40–50 per cent. At this point *Cymbella cymbiformis* increases sharply again to something approaching the degree of dominance shown in the basal lake mud. However, *Anomoeoneis sphaerophora*, an alkalibiont not hitherto very important, now increases greatly. Consequently, the flora of the basal mud is not reproduced as freshwater conditions are re-established, but instead a decidedly more alkalibiontic one occurs.

The small tychoplanktonic *Tetraëdron muticum* (added from the pollen counts) is common in a rather narrowly defined range near the top. This was the only abundant member of the Chlorophyceae to be found in the sediments. Its presence may imply that floating masses of weed (probably *Rhizoclonium*, as in the existing lake) were present in the lake at the time, this being the most usual habitat of this alga.

In the topmost samples small diatoms become increasingly scarce, and all values drop to nearly zero above 165 cm. *Cymbella*, *Epithemia*, and *Anomoeoneis* often appear corroded at this level, and the absence of small diatoms may be due to complete alkali solution. The top few centimetres of calcareous mud and the overlying non-calcareous mud (consisting largely of coarse detritus and root fragments of Cyperaceae, some of which seem to have penetrated it from above) are devoid of diatoms.

Apart from its distinctly alkalibiontic facies, the upper freshwater mud differs in other ways from the basal lake mud. *Gomphonema gracile*, though present, fails to reach abundance. *Cymbella mülleri* and *Fragilaria pinnata* do not reappear but a mixture of *Fragilariae*, apparently referable partly to *F. brevistriata*, partly to *F. similis*, is present instead. *Cymbella mülleri* is a species hitherto unrecorded in South African Quaternary freshwater diatom deposits (Kent and Rogers 1947). It is a common diatom (*fide* Ross) in the Central African lakes, however, and in other tropical fresh waters. Its abundance in the older lake mud of Groenvlei is of considerable interest therefore, though its exact significance is not clear without corroborative climatic evidence. The scarcity of trees and abundance of heath species in the pollen spectrum at this level, however, suggests if anything a drier or more mediterranean climate, not necessarily a warmer or more tropical one.

A comparison of the diatom flora of the freshwater sediments from *c.* 200 cm and upwards, with that obtained from weeds and bottom mud of the present lake (Appendix III) shows other differences, the chief of which is the rarity of *Anomoeoneis* *sphaerophora* in the latter. *Cocconeis clandestina* is commoner than *C. placentula* in the present lake, and *Epithemia zebra* and *Mastogloia elliptica* var. *dansei* are also rather abundant. Apart from the absence of *Campylodiscus clypeus*, this flora resembles the profile flora at *c.* 250 cm more closely, and suggests that the cut-off basin ultimately reached a lower salinity, and possibly a higher pH, than that of the main lake today.

(*c*) *Sedimentation and Productivity*

As all samples utilized approximately equal volumes of sediment, low diatom counts may mean either low productivity or rapid sedimentation, and it is possible to infer which is responsible by consideration of the composition of the sediment column and by comparison with the pollen frequency per unit volume of sediment.

The lower lake muds are particularly rich in diatoms, and owing to the uniformity of both flora and sediment it may be suggested that after a short, initially rapid phase, sedimentation was slow and under very uniform conditions. The formation of telmatic peat terminated this stage. In the ensuing marine stage, there appears to have been a more rapid sedimentation at first, slowing gradually, so that large diatoms increase in frequency per traverse (from 3 per traverse to 15 per traverse). Part of this may be due to the exclusion of *Melosira sulcata* from the total, but it is noticeable that the great burst of *Melosira* (1285 per cent.) at 378 cm is only accompanied by a very slight slump in the frequency of large diatoms (cf. Figs. 6 and 7 at this point), so that the apparent changes in frequency are probably real, if exaggerated. The loss on ignition remains fairly constant, though the carbonate content falls. A possible explanation, then, is that shells and Foraminifera built up the sediment more rapidly below about 450 cm, which led to a dilution of the diatom rain; but a genuine increase in productivity above 450 cm seems more likely, corresponding to the replacement of a warm-water by a more temperate flora.

It may be suggested that the whole of the marine flora represents tidal inwash. This would account in a satisfactory manner for the rather less marine character of the larger microfossils and the macrofossils which accompany the diatoms. If this were so, one would expect the indigenous mesohalobes to show up better when least masked by the marine influx. Evidence is inconclusive; *Amphora proteus* and *Fragilaria construens* var. *subsalina* are the only species whose pattern of distribution in the profile lends support to this view. At the base of the marine section when diatom sedimentation was relatively low, mesohalobes (mainly the above two species) are admittedly relatively slightly more abundant (e.g. Fig. 8 at 510–520 cm), but at 485 cm, though diatoms are equally scarce, the percentage of mesohalobes has much decreased. One would, moreover, be led to the conclusion that influx of marine diatoms reached its highest level (a fivefold increase) immediately prior to the closing of the channel of ingress. The occurrence of two lagoon stages representing successively lower salinity levels is also more reconcilable with a theory of local origin of the majority of marine diatoms, especially as the first of these showed clearly when marine influence was still high.

The sharp fall in productivity during the second lagoon stage of the lake has been noted. There is again no evidence of much more rapid sedimentation. The sediment is somewhat finer, which perhaps suggests deeper water. If the marine flora were to be regarded as wholly allochthonous, this would represent the normal level of autochthonous productivity throughout the entire "marine" period, the L1 to L2 transition representing the point of closing of the lagoon. Above 292 cm the frequency of diatoms equally sharply increases. Here the loss on ignition rises, so that slower sedimentation may be partially responsible. A distinct rise in tree pollen commences just below this level, the chief locus of change in the pollen diagram. An amelioration of climate is suggested as explanation (author, unpublished data). None the less, these changes are of a much smaller order than the changes in diatom frequency, and a fresh rise in productivity under eutrophic freshwater conditions is a probable explanation of the major part of the increase. Above 220 cm, where very calcareous sediment is being laid down, the decrease in diatoms may be due to dilution by more rapid sedimentation. Loss by alkaline corrosion has been suggested for the final dying out of diatoms in the profile. Their absence is unlikely to be due to the development of unfavourable living conditions, as diatoms are still abundant in the present lake.

IV. The Connection of Groenvlei with the Sea

The lakes between the Goukamma River and Wilderness lie in valleys more or less parallel to the coastline, separated by high sandy ridges which are underlain by dune-sand rock (aeolianite) (Martin 1956). The lakes are separated from each other by sand flats, low transverse dunes, and strips of alluvium, the flats mostly not rising to more than 6–8 m above sea-level. Sand ridges commence just west of Wilderness, where they form a narrow belt in front of the lagoon. The width of the dune country and the height of the individual ridges increases eastwards.

Groenvlei, in common with all the lakes not directly connected to rivers, has a large surface area relative to its natural catchment area. The combination of small catchment area, porous soils and substrata, and absence of inflowing streams has no doubt been responsible for the largely autochthonous nature of the sediments in Groenvlei during its freshwater stages. It is separated from Swartvlei by a wide strip of alluvium and sand, the latter forming a ridge the height of which is about 23 m above the lake at its lowest point. From Ruigtevlei, and from the sea, it is separated by multiple aeolianitic ridges rising at the lowest points to about 46 m and at the highest some 180 m above sea-level. This aeolianite framework clearly antedates the present-day lake basin. From the Goukamma River the lake is separated by a 60 m depth of sand which completely blocks the valley eastwards. Thus it seems that its connection to the sea, by analogy with Ruigtevlei, lay through Swartvlei, at least during the latter part of its history (Fig. 9).

At Bleshoender and Sedgefield on opposite sides of Swartvlei there is a distinct terrace-like feature, the surface of which is at about 7–8 m above sea-level, and remarkably flat. The terrace is also seen to the side of the Ruigtevlei valley. The nature of the Sedgefield terrace, as it may be called, is not easily understood from a superficial study because, lying as it does several metres higher than Groenvlei and right across the existing valley, it appears to block the access of the sea that has been demonstrated. Below the level of this terrace are two other levels identifiable in the field; one at 2·5–3 m, a terrace of sandy, more or less podzolized soil bearing

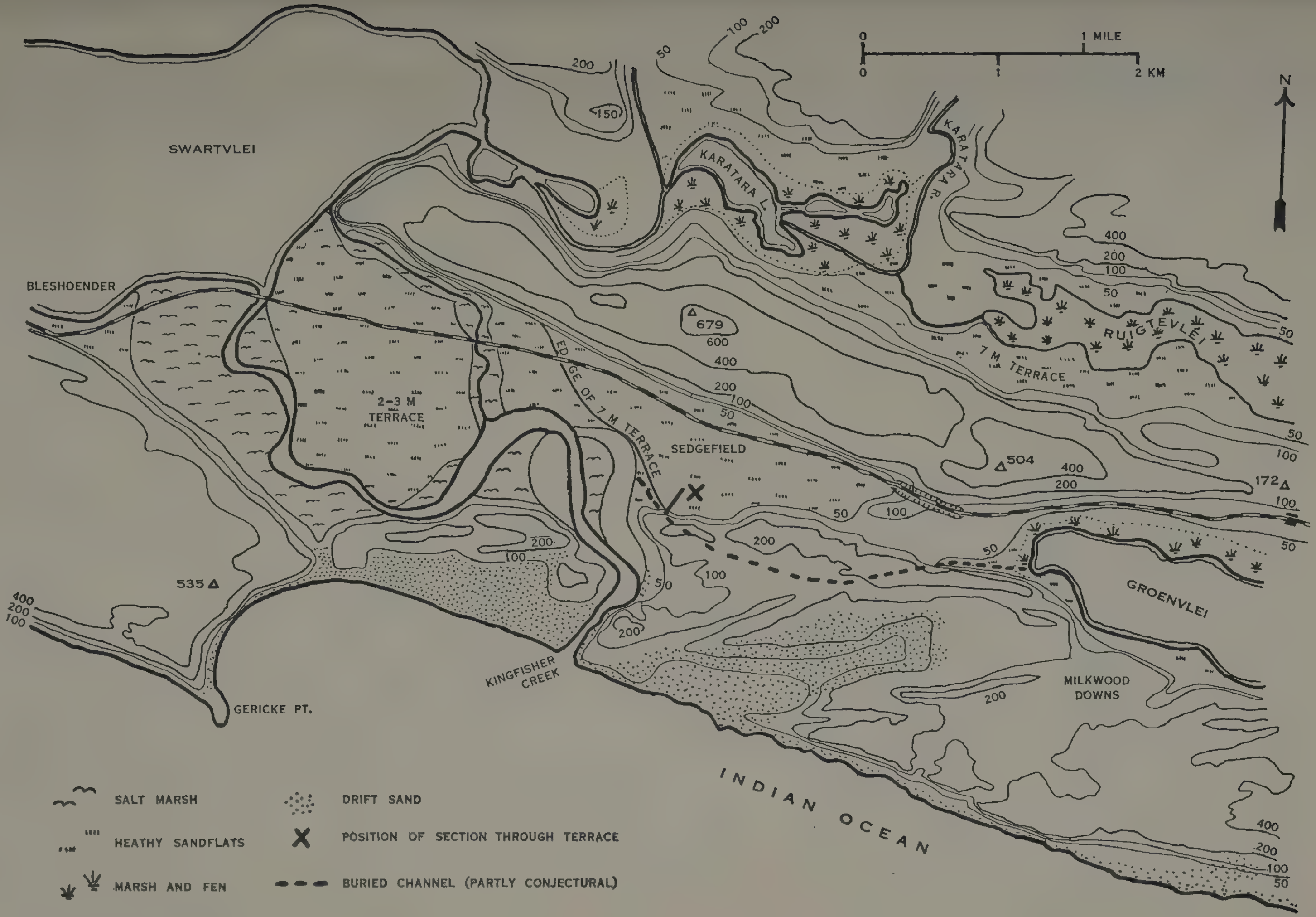

0 1 MILE
0 1 2 KM
N
SWARTVLEI
BLESHOENDER
KARATARA L.
KARATARA R.
RUIGTEVLEI
7 M TERRACE
2–3 M TERRACE
EDGE OF 7 M TERRACE
SEDGEFIELD
679
504
172
535
GROENVLEI
MILKWOOD DOWNS
KINGFISHER CREEK
GERICKE PT.
INDIAN OCEAN
400
200
150
100
50
600
SALT MARSH
HEATHY SANDFLATS
MARSH AND FEN
DRIFT SAND
X POSITION OF SECTION THROUGH TERRACE
BURIED CHANNEL (PARTLY CONJECTURAL)

Fig. 9.—Map of the country between Groenvlei and Swartvlei, showing extent of 7 m and 2·5 m terraces and buried channel connecting Groenvlei to Swartvlei outlet. Contours are in English feet (100 ft = 30·4 m).

open heath. The lowest level is that of the existing tidal mud flats, sparsely colonized by *Arthrocnemum africanum* and *Atriplex patula*, and about 1–1·5 m above sea-level.

The surface soils of the two terraces appear to consist of wind-blown sand. The topmost metre is riddled with the runs of mole rats. Occasional bones of small mammals (? mole rats), shells of land molluscs, and a few artefacts of human origin (pottery fragments, midden piles) indicate the terrestrial origin. These surface soils are underlain by sediment deposited under marine influence. The 7 m terrace consists of about 2–3 m of reddish, weakly podzolized sand overlying a marine or lower estuarine beach which attains a maximum height of 5 m above mean sea-level.

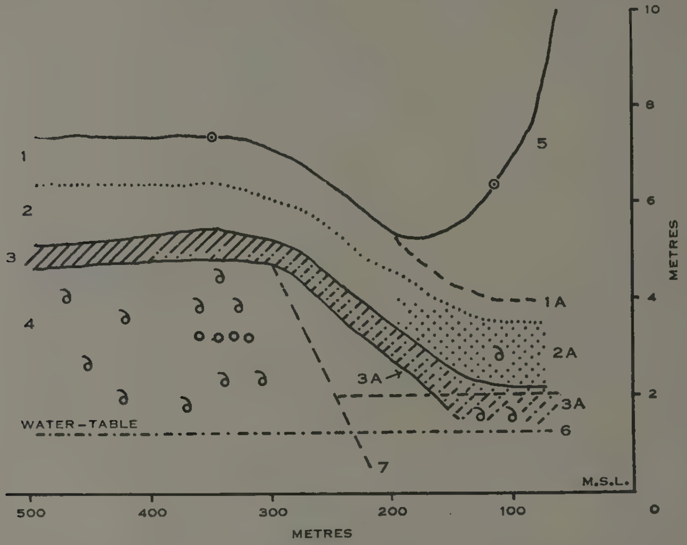


Fig. 10.—Profile of the southern edge of the 7 m terrace at Sedgefield, showing supposed buried Groenvlei channel. Boring could not be carried further south, owing to depth of dune sand. 1, reddish top soil of 7 m terrace. 1A, grey topsoil of 3 m terrace. 2, reddish subsoil of 7 m terrace. 2A, mole-disturbed layer, representing subsoil of 3 m terrace with shells, moved up from below (see Plate 1, Fig. 1). 3, ferruginous podzol horizon of 7 m terrace. 3A, mottled gley podzol horizon of 3 m terrace (catenic with above). 4, shell beach of 7 m terrace. 5, "yellow" calcareous recent dune sand. 6, shells *in situ* in Groenvlei channel deposits. 7, edge of 7 m terrace (conjectural).

The beach sand resembles a clean sea beach, quite free of finer mud or silt, and of a pale yellow-buff colour. A fauna, mainly molluscs, totalling about 70 species is recorded. Dr. K. H. Barnard, reporting on these, describes the assemblage as a typical sandy beach fauna, lacking in many forms common on rocky shores. There is also a small estuarine component evident in such forms as *Nassarius* and *Callianassa*. None are extinct.

The 2·5 m terrace is also underlain by a beach at a depth of about 1 m. Owing to the shallowness of the topsoil, mole rats may bring marine shells to the surface, but the stratigraphy is still fairly clear. The beach of this terrace differs in the abundance in the fauna of *Chione ambigua*, a species absent from the upper beach. The grey-brown, slightly muddy sand is similar to that of the existing Swart estuary.

A number of boreholes were sunk in these terraces and accurately levelled by dumpy level from the bench marks on the National Road where it crosses the terraces. The profile from borings near the southern side of the valley is shown diagrammatically in Figure 10, which indicates the existence of an apparent channel, cut below the level of the 7 m terrace into the 2·5 m terrace, and overlain by a recent dune of unleached, calcareous sand. Plate 1, Figure 1, shows these features and the dry depression representing the channel in the 2·5 m level at Sedgefield. This is evidently the channel from Groenvlei, with a fauna similar to that of the 2·5 m level. It was traced for 800 m at the Groenvlei end, from the lake edge to the point where the dune covers it, and for about 270 m at the Sedgefield end. The intermediate section of about 2000 m is covered by the dune (Fig. 9), but it may be that even before the dune covered it, it was already disused, for about 30 cm of peat which has grown over the channel at the Groenvlei end (Plate 1, Fig. 2) is also being encroached on by the dune. The age of the 7 m terrace cannot at present be judged, though a radiocarbon dating of shells from the 5 m beach at Sedgefield is being sought. The difficulties attending the dating of shell are at present delaying this. The 2·5 m level, however, appears to be a Holocene level and can be traced via the channel deposits back to Groenvlei.

A fuller report on the Quaternary geology of these deposits is in preparation, but a partial explanation appears to be that Groenvlei was first formed during a period of lower sea-level in the upper Pleistocene; that the dunes to north and south became calcified aeolianites; and that a rise in sea-level formed the beach across the end of the valley, but either this beach did not completely block the valley or the sea subsequently broke through again. It is likely that between the episodes of high sea-level, represented by the two terraces, the sea again retreated to a lower level. This could have been, but cannot as yet be proved to have been, the last major eustatic withdrawal to as much as 70 or 100 m below its present level. Some 30 m depth of sedimentary fill has been penetrated in bridging operations at Swartvlei and greater depths in the Knysna estuary to the east, but there is no way of telling at present in which stage of the Pleistocene the channels which they occupy were cut. However, there is no morphological indication of a major cycle of change in sea-level between the formation of the upper and lower terraces. As Groenvlei was at the extreme landward end of the transgression, the sediments there only record the last few metres of the subsequent recovery; the sea could have been rising for some time previously. Borings in the present bed of the lake would probably reveal sediments from earlier stages of the transgression.

There are certain other anomalous features, one of the most important of which is the apparent contradiction (even if it is assumed that all the marine diatoms represent inwash) between the fully marine nature of the diatom flora in the marine mud, and the apparently narrow channel through which the sea entered, if we assume it entered from the Swartvlei direction. It is possible that further evidence will come to light demonstrating either a wider entrance from the Swartvlei end or else a direct opening to the sea, possibly below the Milkwood Downs if the dune rock ridge here should prove incomplete. Any such evidence would be at present buried below a minimum of 30–50 m of drift sand.

Further uncertainty lies in determining the precise level reached by the sea in the Holocene. Unfortunately, owing to the encroachment of sand over the Groenvlei fen basin and over the marine and brackish muds, it is just at the edges, where evidence is most critical, that the boring becomes most difficult. Consequently, only at two points has the apparent margin of the marine transgression sediments been found. None the less, the field data seem to allow of very little latitude of interpretation; compaction may be neglected, as at the margins the transgression muds are lying on sand, not peat, and the likelihood that the sea produced much influence above its present level in the eastern basin of Groenvlei seems slight. However, in a long narrow valley with fresh water entering at the head, freshwater influence will assert itself earlier the nearer the source we search, especially when there is a tendency for the valley to become divided by transverse barrier deposits. A tendency for the eastern end of modern Groenvlei to be less saline than the western end is apparent. It has also been suggested that the diatom flora of the cut-off eastern basin became more oligohalobe in composition than that of the main lake at the present day, while in the east fen basin itself marine sediments appear to pass laterally into brackish. Thus freshwater sediment in the eastern basin might exist contemporaneously with brackish in the main basin or nearer the sea. The oblique profile of the upper end of the lake formed by borings Nos. 6, 7, and 8, the slope of which indicates the dip to the centre of the lake, bears this out (Fig. 4). It will be noticed that the brackish sediments extend higher in Nos. 7 and 8 than in the borings beyond the sand bar (in No. 7, they are 1·5 m above mean sea-level). At the western end of Groenvlei a probe with a hand auger brought up shells of the relatively marine *Dosinia pubescens* from *c.* 1·5 m above mean sea-level, and less than 1 m below the surface of the lake mud. The "*Chione*" fauna of the 1·5 m beach in the lower Sedgefield terrace is therefore to be interpreted as a stronger expression of marine influence nearer the sea, but related to the same level. It is thus not improbable that the sea reached between 1·0 and 1·5 m above its present level, which would be sufficient to produce a tide in the channel, were it unblocked.

V. Correlation and Discussion

The evidence from Bermuda (Sayles 1931), Australia (e.g. Fairbridge 1950; Teichert 1950), and elsewhere has been interpreted as showing that the bulk of the aeolianite was formed prior to and during periods of Glacial recession of the sea, while many Australian workers unhesitatingly correlate the most recent transgression which drowned and terraced this rock, with the European Flandrian. A subsequent slight retreat of the sea is also thought to have been recorded in many parts of the world. Shepard and Suess (1956) obtained no evidence for the post-Glacial stand of the sea higher than at present, finding, for example, an Australian beach deposit at 3–3·6 m (10–12 ft) and supposedly of Holocene age, to be outside the range of radiocarbon dating, whereas Gill (1956) found evidence to the contrary. Such contradictions may be due in some cases to the difficulty of distinguishing in the field between truly Holocene deposits and earlier deposits at very similar levels. For example, the beach in the higher Sedgefield terrace comes well within the range of altitudes for which post-Glacial claims have been made, but on other grounds appears to be older. The present data, allowing for the difficulty in determining precise sea-levels, seem consistent with those of Mabbutt (1954), who produced evidence of a recent stand of the sea at Cape Hangklip, 400 km (245 miles) west of Groenvlei, about 2 m higher than at present. A "5 ft raised beach" at Groot Brak Rivier (Haughton and Visser 1937) 64 km west may also represent such a level. This view of the latter part of the geomorphic sequence could be checked in the present instance by geochronometric methods.

A sample of the freshwater gyttja above the marine transgression was collected by means of a posthole auger, depth 2·9 m (*c.* 9 ft) = *c.* M.S.L.; and a specially constructed large borer of the Hiller type was used to collect a sample of approximately 600 g of wet peat from below the marine transgression, depth 5·8 m (*c.* 19 ft) = *c.* 2·9 m below M.S.L. (Fig. 3). These samples, after careful cleaning, were submitted to the Yale Geochronometric Laboratory for carbon 14 analysis. The dates now available (Deevey *et al.* 1959) are Y466, Groenvlei, lower peat, age 6870 years ±160; and Y467, Groenvlei, upper gyttja (after removal of carbonate), age 1905±60. The initiation of the transgression corresponds well with the opening of the European Atlantic period (Boreal-Atlantic transition) when the post-Glacial eustatic rise of sea-level reached its maximum incidence in many parts of the world (Shepard and Suess 1956; Godwin, Suggate, and Willis 1958). In a general sense, therefore, the sequence at Groenvlei agrees well with the post-Glacial chronology established for other parts of the world. If sedimentation was continuous, the date of 6870 years, though a maximum value, would give a close estimate of the date of flooding, as the sample was from just below the peat/transgression interface. However, it would be necessary to be able to discount the possibilities that either the peat had been truncated by erosion, or that a period of arrest in peat development had supervened. As the whole of the stratigraphic work was completed by use of a peat sampler, it is hard to visualize the true appearance of the peat/mud interface region. The samples from the interface region as brought up in the sampler seem to show a fairly sharp transition between the peat and the mud, extending over only some 5 cm, but the transition becomes less sharp the further eastwards one proceeds. There is no obvious rafting of lumps of peat into the mud. The bottom contours suggest a natural hollow at the point of sampling, in which conditions might be less suited to erosion than in the trough or channel leading to it. The peat immediately below the interface is very well humified, but not noticeably more so than further down the profile, and the occurrence of the semi-aquatic moss *Leptodictyum riparium* throughout does not suggest a drying out of the peat surface. Finally, there is no obvious corrosion of pollen grains in the peat just below the interface, such as would indicate a period of drying out and oxidation prior to the flooding. Thus there is no evidence pointing to a hiatus at this level.

Neither is there any clear evidence of a hiatus between 5·8 and 2·9 m, the exact nature of the marginal reddish muds described in Section II being in doubt; even if they represent marginal oxidation there is no evidence of a cessation of sedimentation in the centre. There could therefore have been a lapse of some 5000 years between the onset of transgression and the re-establishment of a freshwater lake, during which only some 3 m of sediment was laid down, an average of 6 cm per century. Excessive in duration though this may seem, no long break in deposition can be demonstrated. However, it is known that truncation of profiles, especially as interpreted from borehole data, may fail to reveal itself, and it is felt that while at present there is no evidence which appears to favour this view, the opposite view should be accepted only with caution.

Radiocarbon-dated evidence from south-eastern Australia (Gill 1956) suggests a major eustatic rise in sea-level, referable to the same period as the Groenvlei transgression. A *Eucalyptus* tree stump in position of growth at 63 ft (19 m) below low water at Spencer Street, Melbourne, proved to be about 8780 years old; while a sample of wood bored by *Teredo*, from some 7 miles (11 km) up the Maribyrnong River, Melbourne, and hence above present sea-level, had an age of approximately 4800 years. The first of these, earlier than the record of sedimentation at Groenvlei, indicates a sea-level well below the present one, correlated with vegetational evidence thought to indicate a wetter and colder climate. There is a suggestion here of general correspondence with the European pre-Boreal or early Boreal period. Godwin, Suggate, and Willis (1958) demonstrate the eustatic recovery for the Christchurch area of New Zealand, while results essentially identical with those from Groenvlei have also been obtained at the mouth of the Rio Negro, south of Bahia Blanca, Argentina (Deevey *et al.* 1959). The stratigraphy is described by Auer (1951, 1956). These various data suggest conformity in the dates at which the post-Glacial oceans reached similar levels in different parts of the southern hemisphere and conformity in the general rate of eustatic recovery, and, thereby, essential crustal stability at least in these four widely separated areas. If further substantiated, this would have importance in the use of this type of data for correlation in other areas where stability could be assured, and in the study of historical ecology of coastal plant formations in such areas.

VI. Acknowledgments

Mr. R. Ross (British Museum, Natural History) is warmly thanked for placing facilities at my disposal, for guidance in naming diatoms, and for helpful discussion of the problem; also Dr. K. H. Barnard (South African Museum), for nomenclature of shells and for discussion of the Sedgefield data. My thanks are due to Mr. F. S. C. Rogers of Sedgefield, for the detailed levelling recorded in this paper, and to the Director of the Trigonometrical Survey, Pretoria, for supplying information incorporated in Figure 9. Thanks are also tendered to the Council for Scientific and Industrial Research, Pretoria, for grants by which field work was made possible, and to the Royal Commission for the Exhibition of 1851 for the grant of an Overseas Scholarship by which the detailed study was furthered during 1953 and 1954. My thanks go to Professor W. H. Pearsall for his supervision of the work during that period. Professor E. S. Deevey kindly supplied pre-publication information regarding ^{14}C dates at Groenvlei and Rio Negro.

My thanks go to my wife for assistance at all stages of the work and for typing the manuscript.

STRATIGRAPHY AND HISTORY OF GROENVLEI

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EXPLANATION OF PLATE 1

Fig 1.—The lower terrace (2·5–3 m) at Sedgefield, with the upper terrace (7 m) at rear. Recent dune in background. Approximate position of the profile of Fig. 10 shown at X. Note also the depression in the lower terrace, indicating former stream channel. Mole activity in this terrace is noticeable at right, above centre.

Fig. 2.—Old channel sediments under shallow peat, *c.* 600 m west of Groenvlei.

APPENDIX I

Foraminifera and Ostracoda from Groenvlei muds (boring H.I)

Preliminary report by Dr. T. Barnard and Mr. A. J. Lloyd

Depth (cm)	Foraminifera	Ostracoda
160	(Small sample) *Rotalia* few	 "*Cythere*" *A* rare
315	*Rotalia* abundant	*Paracypris* abundant "*Cythere*" *A* few
345	*Rotalia* abundant *Elphidium* common *Triloculina* very rare *Quinqueloculina* very rare	*Paracypris* few "*Cythere*" *A* rare
376	(Small sample) *Rotalia* very rare *Elphidium* very rare	 "*Cythere*" *A* very rare
454	*Rotalia* abundant *Bolivina* common *Elphidium* common	"*Cythere*" *B* common
498	*Rotalia* abundant *Triloculina* frequent *Elphidium* common *Bolivina* frequent	*Paracypris* common "*Cythere*" *B* few

The Foraminifera are mostly brackish water forms of wide tolerance—*Rotalia* and *Elphidium* spp.; the rarer types *Triloculina* and *Quinqueloculina* are more marine, and *Bolivina*, common only in the lowest samples, is also essentially marine. "*Cythere*" *B* is thought to be a marine species.

The positions of the samples are indicated on the sedimentary column in Figure 8.

Appendix II

Laboratory Investigation of Diatoms

Small samples of approximately equal volume were obtained by pushing a glass tube to a fixed depth, marked by a notch on the tube, into a cut transverse surface on the sediment cores. The material was transferred to a centrifuge tube; carbonate was removed with dilute hydrochloric acid, and organic matter by treatment with a mixture of equal parts of concentrated nitric and hydrochloric acids, to which a few crystals of sodium chlorate were added, followed by boiling. Diatoms were concentrated by centrifuging, washed four times in distilled water and twice in alcohol, and all samples made up to an equal volume in absolute alcohol. Equal volumes of the suspension were transferred to coverslips and dried over a lamp bulb. Samples were mounted in "Clearax"; counts were made under oil immersion, 150 diatoms greater than 40 by 7 μ being counted in each sample to form the 100 per cent. sum, and small species were expressed outside this sum.

After counting the 150-total, in well-spaced traverses, the whole preparation was examined under low power and any additional large species were given + values. Where valves remained together in pairs or a number of individuals of a colony remained attached, each was counted separately. Intercalary bands were omitted, but septa of *Grammatophora* were counted, as they usually outnumbered the delicate, easily broken valves. The fragmentary lengths of long diatoms such as *Synedra* spp. were added together and divided by the length of an average individual to obtain a count.

APPENDIX III

Groenvlei: Diatoms from Surface Muds and Weeds

Samples:

(1) Superficial mud (calcareous) from landing stage, c. 30 cm of water.
(2) Superficial mud consisting almost entirely of *Chara* spicules.
(3) Superficial mud (calcareous) from c. 2·6 m of water off boathouse.
(4) Cladophoraceae bearing epiphytes.
(5) *Chara* bearing epiphytes.

Frequency classes: a, abundant; c, common; f, frequent; o, occasional; r, rare; v.r., very rare.

Halobion classes: E, euhalobic; M, mesohalobic; H.phil, halophilous oligohalobe; Ind., indifferent oligohalobe.

pH classes: Alkbiont, alkalibiontic; Alkphil, alkaliphilous; Ind., indifferent.

Lake type: O, oligotrophic; E, eutrophic.

Species*	Samples					Halobion Class	pH Class	Lake Type
	1	2	3	4	5			
Achnanthes minutissima	c	f	o-f	c	o-f	Ind.	Ind.	O-E
A. ? cf. *lemmermannii*	—	r	—	?	—			
A. microcephala	—	—	—	o	—	Ind.		
Achnanthes sp.	—	v.r.	—	—	v.r.			
Amphora cf. *coffeaeformis*	o	o-f	r-o	f	f-c	M		
A. exigua	o	o	r	o	r-o	E-M		
A. veneta	r-o	v.r.	r	v.r.	v.r.	Ind.	?	
Anorthoneis sp.	—	r	v.r.	v.r.	r			
Anomoeoneis sphaerophora	r	r	r-o	v.r.	—	Ind.	Alkbiont	E
Campylodiscus clypeus	v.r.	—	v.r.	—	v.r.	M		
Cocconeis clandestina	a	a	o-f	c	a	?M		
C. placentula	v.r.	r	v.r.	—	r	Ind.	Alkphil	O-E
Cyclotella meneghiniana	r	r	r	—	—	H.phil	Alkphil	E
Cymbella cymbiformis	c	c	f	—	f	Ind.	Alkphil	E
C. microcephala	o-f	f	o	—	o	Ind.	Alkphil	E
C. microcephala f. *minor*	a	a	a	—	o			
C. pusilla	c	f-c	o	f-o	c	H.phil	Ind.	
Diploneis ovalis var. *oblongella*	—	o	—	—	v.r.	Ind.		
Epithemia zebra	c	f	c	v.r.	f	Ind.	Alkphil	E
Fragilaria cf. *similis*	r	r	—	v.r.	v.r.			
Gomphonema gracile	v.r.	r-o	—	v.r.	r	Ind.	Ind.	O-E
Mastogloia elliptica var. *dansei*	c	f	c	o	f	H.phil	?	?
M. braunii	—	v.r.	—	r	r-o	M		
M. smithii var. *lacustris*	v.r.	v.r.	—	r	r	Ind.		
Navicula cincta	—	r-o	—	r	r	H.phil	Alkphil	E
N. cryptocephala	o	o	r	v.r.	o	Ind.	Alkphil	O-E
N. gregaria	o	r	v.r.	v.r.	—	H.phil-M		
N. cf. *incerta* (or *salinicola*)	—	f	r	o	f-c	M		
N. oblonga	r-o	r-o	o	—	v.r.	H.phil	Alkphil	E
N. pupula	r	r	—	—	—	Ind.	Ind.	E
N. radiosa	—	r-o	—	—	v.r.	Ind.	Ind.	O-E
Nitzschia amphibia	r-o	o	o	—	r-o	Ind.	Alkbiont	E
N. fonticola	o-f	o	r	r	r	Ind.	Alkphil	E
N. kützingiana	o-f	o-f	r	r	f	Ind.	Alkphil	E

APPENDIX III (*Continued*)

Species*	Samples					Halobion Class	pH Class	Lake Type
	1	2	3	4	5			
N. cf. *linearis*	v.r.	?	—	—	?	Ind.	?	?E
N. microcephala	o	o-f	—	o	o	H.phil	Alkphil	E
N. cf. *sublinearis*	—	o	—	o	?			
Opephora pacifica var. *parva*	—	r	—	—	—	M		
Pleurosigma elongatum	v.r.	v.r.	v.r.	—	r	M		
?*Rhaphoneis* sp.	v.r.	r	—	—	—			
Rhopalodia gibba	o	f	o-f	r	o-f	Ind.	Alkphil	E
R. gibberula	—	r	—	—	r-o	M		
Synedra acus	r	o	r	v.r.	r	Ind.	Ind.	E
S. tabulata	—	v.r.	—	—	r	H.phil-M		
S. cf. *tenera*	—	o	r	a	o-f	?Ind.	?Alkphil	E
S. ulna	—	v.r.	r	—	—	Ind.	Alkphil	O-E

*Nomenclature of diatoms in general follows standard recent treatments. The following species may not appear in such works: *Actinoptychus janischii* Grun. (this appears to be distinct from *A. splendens* (Shad.) Ralfs., with which the name is usually regarded as synonymous); *Amphora eulensteinii* Grun. (= *A. angusta* Greg. var. *eulensteinii*); *Fragilaria similis* Krasske (1938).

STUDIES ON THE *SARCOMENIA* GROUP OF THE RHODOPHYTA

By H. B. S. Womersley* and E. Ann Shepley*

[*Manuscript received November* 13, 1958]

Contents

		Page
	Summary	168
I.	Introduction	169
II.	Material and methods	169
III.	The species placed under *Sarcomenia* Sonder	171
	1. *Sarcomenia delesserioides* Sonder	171
	2. *S. victoriae* Harvey ex J. Agardh	176
	3. *S. corymbosa* J. Agardh	182
	4. *S. hypneoides* Harvey	185
	5. *S. mutabilis* (Harvey) J. Agardh	187
	6. *S. tenera* (Harvey) J. Agardh	188
	7. *S. dolichocystidea* J. Agardh	191
IV.	Other taxa allied to *Sarcomenia*	194
	1. *Platysiphonia miniata* (C. Agardh) Boergesen	194
	2. *Cottoniella* Boergesen	199
	3. *Cottoniella hawaiiensis* Doty & Wainwright	202
	4. *Polysiphonia roeana* Harvey	204
	5. *Taenioma* J. Agardh	205
V.	The distinctive features of the *Sarcomenia* group	206
VI.	The genera and species of the *Sarcomenia* group	207
	Key to genera of the *Sarcomenia* group	208
	Key to the species of *Platysiphonia*	209
	Key to the species of *Sarcotrichia*	210
VII.	Taxonomic relationships of the *Sarcomenia* group	211
VIII.	Phylogenetic relationships of the Sarcomenioideae	218
IX.	Other genera possibly related to the Sarcomenioideae	220
X.	Acknowledgments	221
XI.	References	221

Summary

A study of species placed in the genus *Sarcomenia*, and study of allied genera, shows that *Sarcomenia* includes one species only, *S. delesserioides* Sonder. Other species belong either to *Platysiphonia* Boergesen or to *Sarcotrichia* gen. nov. The Australian *Polysiphonia roeana* is shown to belong to the *Sarcomenia* group and is placed in a new genus, *Malaconema*. Other related genera which are discussed are *Cottoniella* Boergesen and *Taenioma* J. Agardh. *C. hawaiiensis* Doty & Wainwright is placed in a new genus, *Dotyella*.

These genera form a uniform group, distinguished largely on vegetative features since their reproductive structures are very similar. The *Sarcomenia* group forms an intermediate and linking group between the Delesseriaceae and Rhodomelaceae, but shows somewhat more features in common with the latter family and may have been derived from rhodomelaceous ancestors. The group is recognized as a subfamily, the Sarcomenioideae, of the Rhodomelaceae, and all other groups of the Rhodomelaceae are considered to form a second subfamily, the Rhodomeloideae. Phylogenetic relationships of the Sarcomenioideae are discussed.

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I. Introduction

The *Sarcomenia* group has been recognized as an entity since the tribe Sarcomenieae was first described by J. Agardh (1863), but its systematic position, and more recently the genera it includes, have been much debated. Agardh placed the *Sarcomenia* group in the Rhodomelaceae and included the following genera: *Sarcomenia*, *Taenioma*, *Vanvoorstia*, and *Claudea*. Although Agardh (1896, pp. 120–37; 1899, pp. 130–49) strongly maintained the rhodomelaceous affinities of the group, Schmitz (1889), Schmitz and Hauptfleisch (1897), and in particular Falkenberg (1901), were equally emphatic that the group belonged to the Delesseriaceae.

More recent authors have usually agreed with the delesseriaceous position of the *Sarcomenia* group, but Papenfuss (1937) split off *Claudea*, *Vanvoorstia*, and *Caloglossa* as the *Claudea* group of the Delesseriaceae. Kylin (1956) recognizes *Sarcomenia*, *Taenioma*, *Platysiphonia*, *Cottoniella*, and *Sonderella* as members of the *Sarcomenia* group.

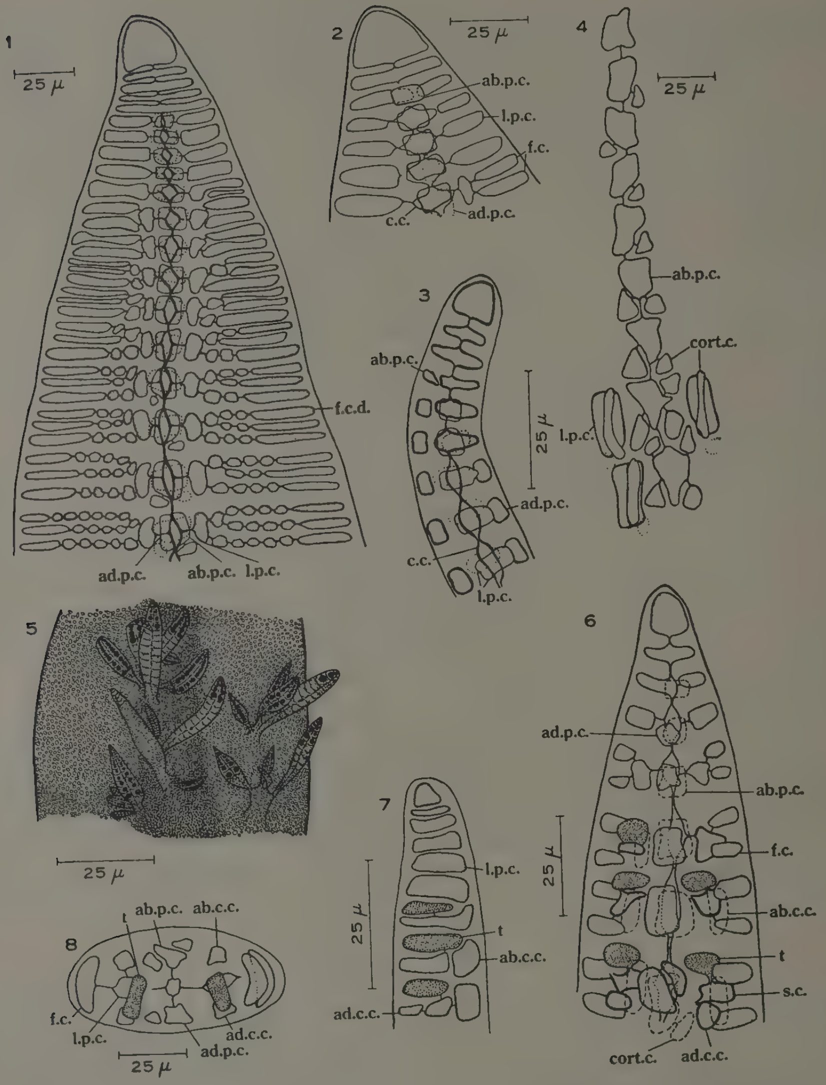
It is most noteworthy that only J. Agardh examined *Sarcomenia* in any detail. Falkenberg studied *Taenioma* as an example of the group, as also did Papenfuss (1944). Recent views on the position of the *Sarcomenia* group have thus not been based on the genus after which the group was named, and therefore are not well founded. This is in large measure due to the difficulty in studying dried material of *Sarcomenia* and allied genera, since they adhere closely to paper and largely disintegrate on being soaked off the paper. No species of *Sarcomenia* has been studied in full detail previously.

This study, based on adequate liquid-preserved material, was undertaken to clarify the position of the *Sarcomenia* group and its relationships to the Delesseriaceae and Rhodomelaceae. The genera investigated are those currently recognized by Papenfuss (1937) and Kylin (1956) after segregation of the *Claudea* group, with the exclusion of *Sonderella* Schmitz. This genus proves to be a member of the Rhodomelaceae allied to the *Amansia* group, and its structure and reproduction will be described in a separate paper.

II. Material and Methods

In most cases the material was preserved in 4 per cent. formalin–sea-water. No liquid-preserved material of certain species was available but the essential features were studied from herbarium specimens after brief soaking in detergent and careful removal from the paper. In general 1 per cent. aqueous aniline blue ($\frac{1}{2}$ min to a few minutes) fixed in dilute hydrochloric acid, was found to be an excellent stain. After washing, selected fragments were mounted directly in 50 per cent. Karo syrup, or, if more delicate, placed in 20 per cent. Karo syrup which was allowed to concentrate before mounting. Such mounts hardened considerably over a few weeks and proved much superior to glycerine mounts.

For studies of the segmentation of the lateral pericentral cells of the stichidia, to form the tetrasporangia and cover cells, the material was cleared in 5 per cent. potassium hydroxide and a whole branch mounted. Stichidia lying on edge could then be studied in optical longitudinal section, but in general the sequence of divisions


1
25 μ
f.c.d.
ad.p.c.
ab.p.c.
l.p.c.
2
25 μ
ab.p.c.
l.p.c.
f.c.
c.c.
ad.p.c.
3
ab.p.c.
25 μ
ad.p.c.
c.c.
l.p.c.
4
25 μ
ab.p.c.
cort.c.
l.p.c.
5
25 μ
6
ad.p.c.
ab.p.c.
25 μ
f.c.
ab.c.c.
t
s.c.
cort.c.
ad.c.c.
7
l.p.c.
25 μ
t
ab.c.c.
ad.c.c.
8
t
ab.p.c.
ab.c.c.
f.c.
l.p.c.
ad.c.c.
ad.p.c.
25 μ

Figs. 1–8.—*Sarcomenia delesserioides.* Fig. 1.—Branch apex, showing formation of lateral chains of cells. Fig. 2.—Apex, showing segmentation. Fig. 3.—Side view of apex, showing formation of abaxial and adaxial pericentral cells. Fig. 4.—Development of cortication from the abaxial pericentral cells. Fig. 5.—Portion of thallus bearing stichidia. Fig. 6.—Upper part of a stichidium, showing formation of tetrasporangia and cover cells. Fig. 7.—Optical longitudinal view of a young stichidium, showing division of the lateral pericentral cells into a tetrasporangium and cover cells. Fig. 8.—Transverse view of a stichidium.

[*For meaning of abbreviations see opposite page.*]

could only be observed in very young stichidia. Older stichidia always showed formation of tetrasporangium and both cover cells between one segment and the next.

III. The Species Placed under Sarcomenia Sonder

J. Agardh (1899, p. 148) recognized 13 species of *Sarcomenia*, 12 of which were Australian (including *S. miniata*). Of these 4 have proved to be synonymous with other species, leaving 7 species under *Sarcomenia*, plus *Platysiphonia miniata*. All these species are discussed below. *S. rhizocarpa* Harvey (1863, synop. No. 188) is probably a species of *Dasya*.

1. **Sarcomenia delesserioides** Sonder 1845: 56; 1846: 194. J. Agardh 1863: 1266; 1896: 137; 1899: 140. De Toni 1900: 742; 1924: 361. Harvey 1847: 21; 1854: 537; 1860: pl. 121. Kuetzing 1849: 880.

Figs. 1–19; Plate 1, Fig. 1

Type locality.—Western Australia (*Preiss* 2618).

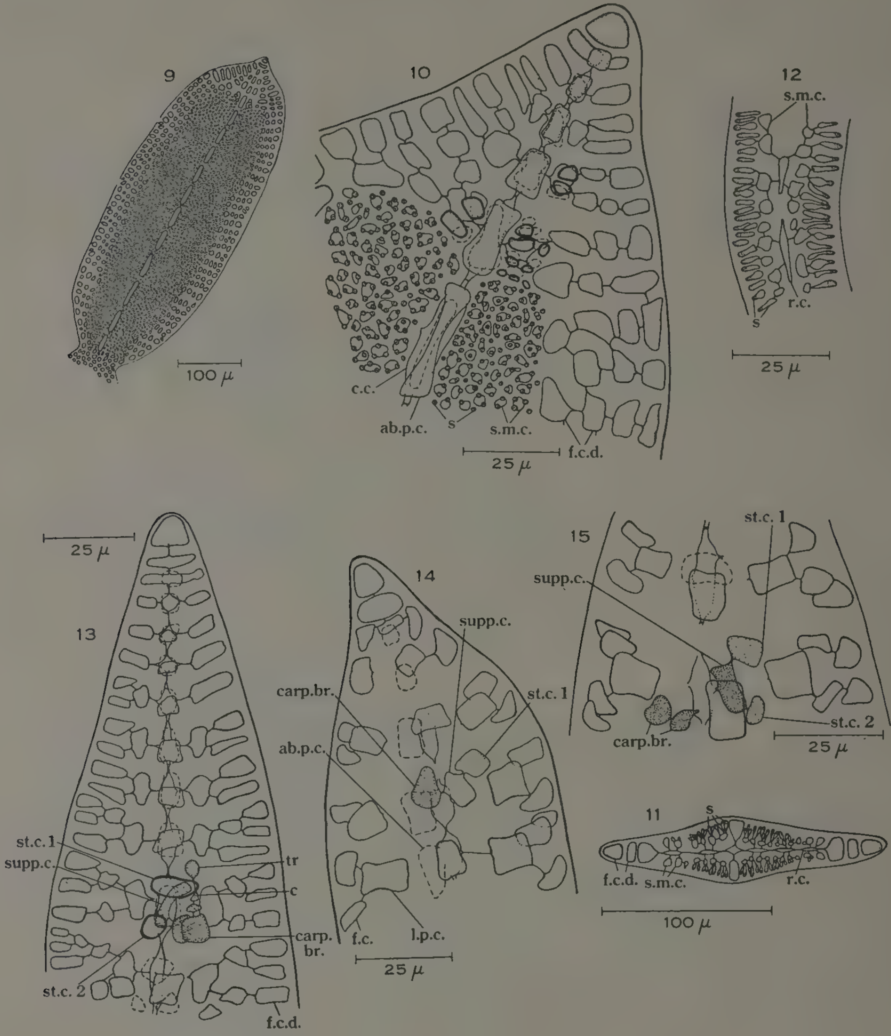
Type.—MEL (herbaria are abbreviated according to Lanjouw, J., and Stafleu, F. A. (1952).—"Regnum Vegetabile. Vol. 2. Index Herbariorum. Pt. I. The Herbaria of the World").

Distribution.—From Fremantle, W.A., to Western Port, Vic. Sublittoral on rough coasts.

Sarcomenia delesserioides, the type species of the genus, was described by Sonder in 1845 from material collected by Preiss on the south-west coast of Western Australia. The thallus is considerably larger than that of any other member of the group and is rather variable in width and degree of branching. It reaches 50 cm in height and may, in its older parts, attain a width of 2·5–3 cm. Most plants occurring around southern Australia are about 1 cm in width (Plate 1, Fig. 1). In some plants the branches terminate in curled tendrils. Intergrades between plants with broad and narrow thalli are common and it is difficult to delimit distinct forms as suggested by Harvey (1860, Plate 121). Lateral branches occur on both abaxial and adaxial surfaces (more commonly on the latter) at a position usually between midrib and margin. They arise endogenously from the central cells of the parent branch, but their point of origin from the thallus is displaced by later growth. Tetraspores, spermatia, and carpogonial branches occur on small blades (Figs. 5, 9) which develop similarly to lateral branches. The thallus, when fresh, has a greyish red iridescence, but on exposure to air or soon after collection changes to a bright rosy red colour and decomposes rapidly.

Abbreviations Applying to All Text Figures

ab.c.c., Abaxial cover cell; *ad.c.c.*, adaxial cover cell; *ab.p.c.*, abaxial pericentral cell; *ad.p.c.*, adaxial pericentral cell; *aux.c.*, auxiliary cell; *c*, carpogonium; *carp.br.*, carpogonial branch; *c.c.*, central cell; *cort.c.*, corticating cell; *f.c.*, flanking cell; *f.c.d.*, flanking cell derivative; *fus.c.*, fusion cell; *gon.fil.*, gonimoblast filament; *gon.init.*, gonimoblast initial; *l.p.c.*, lateral pericentral cell; *r.c.*, residual cell; *s*, spermatangium; *s.c.*, stalk cell; *s.m.c.*, spermatangium mother cell; *st.c.* 1, first sterile cell; *st.c.* 2, second sterile cell; *supp.c.*, supporting cell; *t*, tetrasporangium; *tr*, trichogyne.


9
100 μ
10
c.c.
ab.p.c.
s
s.m.c.
f.c.d.
25 μ
12
s.m.c.
r.c.
s
25 μ
25 μ
13
st.c. 1
supp.c.
tr
c
carp. br.
st.c. 2
f.c.d.
14
supp.c.
carp.br.
ab.p.c.
st.c. 1
f.c.
l.p.c.
25 μ
15
st.c. 1
supp.c.
carp.br.
st.c. 2
25 μ
11
s
f.c.d.
s.m.c.
r.c.
100 μ

Figs. 9–15.—*Sarcomenia delesserioides*. Fig. 9.—Mature spermatangial blade. Fig. 10.—Tip of spermatangial blade, showing development of spermatangial mother cells and spermatangia. Fig. 11.—Transverse section of spermatangial blade. Fig. 12.—Longitudinal section through lateral pericentral cell region of spermatangial blade. Fig. 13.—Young blade of a female plant, showing carpogonial branch and 2 sterile cells. Fig. 14.—Early development of a carpogonial branch, with the first sterile cell and carpogonial branch initial cut off from the supporting cell. Fig. 15.—A carpogonial branch at a 2-celled stage (slightly displaced), with 2 sterile cells.

Material on which these investigations have been carried out was collected, as drift, at Port McDonnell and Nora Creina Bay, S.A. (tetrasporic plants only) in August 1953 (AD: A19016); at Robe, S.A. (spermatangial and young cystocarpic plants) in March 1955 (AD: A19870); and at Nora Creina Bay, S.A. (mature cystocarpic plant) in November 1955 (AD: A21394).

Structure of thallus

Growth is initiated by a hemispherical apical cell, which cuts off cells posteriorly. In the third or fourth segment, a cell is cut off from the abaxial surface, forming the abaxial or dorsal transverse pericentral cell (Figs. 1–3). Two cells are next cut off laterally to form the lateral pericentral cells. No strict order for the formation of these 2 lateral cells has been observed. Shortly after the formation of the 2 lateral pericentral cells, a cell is cut off from the adaxial surface, thus forming the fourth pericentral cell (Figs. 2, 3). This order of pericentral cell development is that typical of the Rhodomelaceae and the abaxial pericentral cells are formed in a line. The lateral pericentral cells elongate and 2 cells (one anterior to the other) are cut off from each so as to leave a lateral pericentral cell of about the same size as the transverse pericentral cells (Figs. 1, 2). The upper of these 2 flanking cells again divides in the same way. Thus 3 elongate cells are produced from each lateral pericentral cell and further divisions occur at the inner edges of these, forming lateral chains of cells, always with an elongate cell at the edge of the blade. After the formation of the 4 pericentral cells as described above, a portion of the original saucer-shaped cell remains, forming the central cell (Figs. 1, 3). Central cells of successive segments are connected by large, distinct pit connections. Thin protoplasmic connections are visible between all other cells and their derivatives. In older parts of the thallus secondary pit connections develop, firstly between adjacent pericentral cells and later between the cells of the lateral chains.

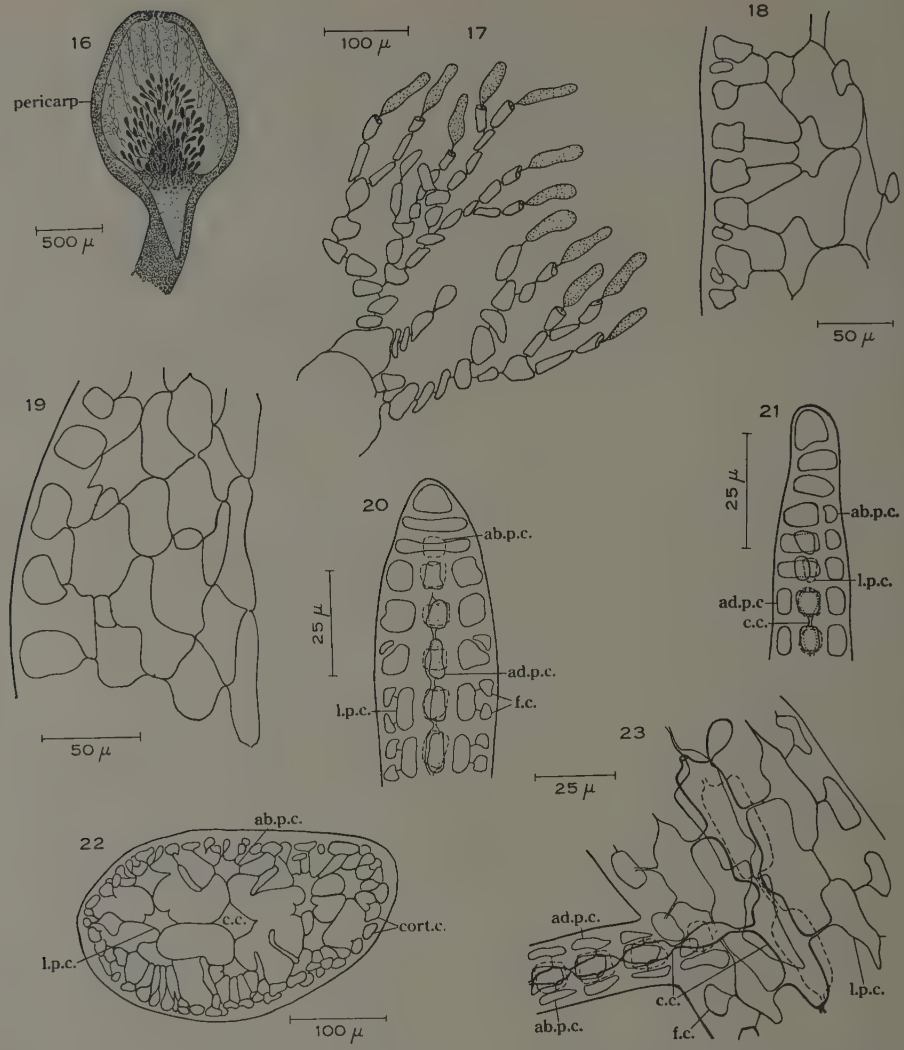
Cortication of the thallus begins usually about 20 segments from the tip. The transverse pericentral cells cut off, by an oblique wall, a small cell at 1 posterior corner of the pericentral cell (Figs. 1, 4). Such cells are cut off at alternate posterior corners of successive pericentral cells. At a later stage a cell is cut off at the other posterior corner and later still, 2 cells are cut off at the anterior corners of these pericentral cells. At about the 25th segment cortication of the lateral pericentral cells commences, cells being cut off by periclinal divisions on both sides of the blade. Complete cortication occurs by similar periclinal divisions of all the lateral cell chains of the blade (Fig. 5).

Lateral branches arise endogenously from the central cells of a parent blade. The anterior end of a central cell cuts off a cell which acts as an apical initial, emerging to one side of the transverse pericentral cell and developing pericentral cells itself as described above.

Development of stichidia and tetrasporangia

Tetraspores are produced in small lateral blades or stichidia, which arise singly or in groups of up to 6. These groups are formed by younger stichidia developing at the base of an older one; often only the base of the older stichidium remains (Fig. 5). The tetrasporangia are formed in 2 regular, vertical rows in the stichidium and mature in acropetal succession (Figs. 5, 6). Stichidia are endogenous in origin, and cell development is similar to that of lateral branches.

However, the 2 derivatives (flanking cells) of each lateral pericentral cell do not divide to form chains of cells though each cuts off a small cell anteriorly. Thus there are 4 cells at the edge of the blade corresponding to each segment of the thallus.


16
pericarp
500 μ
100 μ
17
18
50 μ
19
50 μ
20
ab.p.c.
25 μ
ad.p.c.
l.p.c.
f.c.
21
25 μ
ab.p.c.
l.p.c.
ad.p.c.
c.c.
22
ab.p.c.
c.c.
cort.c.
l.p.c.
100 μ
23
25 μ
ad.p.c.
l.p.c.
c.c.
ab.p.c.
f.c.

Figs. 16–19.—*Sarcomenia delesserioides.* Fig. 16.—Sectional view of a mature cystocarp. Fig. 17.—Upper part of the carposporophyte with terminal carposporangia. Fig. 18.—Transverse section of pericarp. Fig. 19.—Longitudinal section of pericarp. Figs. 20–23.—*Sarcomenia victoriae.* Fig. 20.—Tip of branch, showing cell segmentation. Fig. 21.—Side view of branch apex, showing development of transverse pericentral cells. Fig. 22.—Transverse section of a mature branch. Fig. 23.—Formation of a lateral endogenous branch.

These outer cells become curved and elongate horizontally, thus forming a protective covering around the developing tetrasporangium (Fig. 8).

The lateral pericentral cell cuts off the sporangium and 2 cover cells in very rapid succession. In all but the youngest stichidia they are all formed in passing from one segment to the next. Several very young stichidia were observed, however, in which the sporangium was first cut off by a curved wall (Fig. 7) in such a way that it was exposed on the adaxial side of the stichidium but protected on the abaxial side by an extension of the old pericentral cell. The abaxial (dorsal) cover cell is next cut off, and still protects the sporangium on that side. The abaxial (ventral) cover cell is cut off last and remains small so that the sporangia are more or less exposed on that side of the stichidium (Figs. 6, 7).

As the tetrasporangium develops, the cover cells and flanking cells enlarge but the stalk cell becomes considerably stretched laterally, forming a very thin yet conspicuous cell in the stichidium. The tetraspores, which are tetrahedrally arranged, are liberated from the adaxial surface of the blade and after their liberation the cover cells undergo division to form small groups of cells which later merge with the general cortication of the old stichidium. Owing to the acropetal formation of the tetrasporangia, in one stichidium there are usually immature and mature tetrasporangia as well as the corticated basal region from which the tetraspores have been shed.

Development of spermatangial blades

Spermatangial blades develop endogenously from the central cells. Although these blades often appear to arise from the lateral wing of the branch, their central cell row can always be traced back, within the thallus, to the central cell row of the parent branch. As in normal branch development 3 marginal cell initials are formed at each edge of a segment, and in the spermatangial branches these undergo limited division, forming short lateral chains of cells. Thus a narrow winged blade is produced (Figs. 9, 10). The lateral pericentral cells cut off by obliquely periclinal walls 2–4 cortical cells (on each surface), each of which divides by anticlinal walls into 4 or more cells. The number of divisions in each of these series is variable, but ultimately a block of about 16 cells lying in the surface plane is formed. These are the spermatangial mother cells, each of which cuts off 2–4 elongate spermatangia (Figs. 10–12). The distal ends of these cells are densely protoplasmic and become rounded and budded off as spermatia (Fig. 12).

Although spermatangia production commences from the lateral pericentral cells, it gradually spreads outwards to involve the inner cells of the lateral wing of the spermatangial blade. However, a sterile margin of 3–4 undivided cells is maintained surrounding the spermatangial cells (Figs. 9, 10). The transverse pericentral cells take no part in spermatia production, but remain as a sterile "midrib" of cells in each spermatangial blade (Fig. 9). A small amount of cortication develops at the base of the spermatangial blade where it unites with the parent branch.

Development of procarp

Carpogonial branches form in small fertile blades which are similar to a lateral branch but show only limited division of the 3 lateral initials in each segment. The carpogonial branches develop only from the adaxial transverse pericentral cell. In a fertile segment, the adaxial pericentral cell first cuts off a cell towards its anterior end (Fig. 14). This is the first "sterile cell", and comes to lie horizontally across the anterior end of the central cell (Fig. 13). Following this, another cell is cut off laterally from the adaxial pericentral cell, this being the carpogonial branch initial (Fig. 14). Thus the adaxial pericentral cell itself functions as the supporting cell of the carpogonial branch. By the time the carpogonial branch has become 2-celled, a second sterile cell is cut off laterally, on the opposite side of the supporting cell to the carpogonial branch (Fig. 15). The mature carpogonial branch is 4-celled, the second cell being the largest, and the small carpogonium bears a very short trichogyne, terminating in a large globular head (Fig. 13).

Development of cystocarp

Changes taking place immediately following fertilization have not been studied, as only fully mature cystocarps have been observed. These are produced adaxially from small branchlets formed on both surfaces of the blade. Since the procarps develop near the apex of the fertile branchlets, the cystocarps appear pedicellate. The cystocarp wall is considerably corticated except for the cells around the ostiole. The inner layer of the pericarp is composed of vertical chains of cells, from each of which usually 2 cells are produced externally. Each of these outer cells cuts off several smaller cortical cells and these produce another layer of small cells which form the outer layer of the pericarp. Thus the pericarp wall is composed of 4 layers of cells (Figs. 16, 18, 19)—the inner vertical rows of cells, developing from the pericarp initials, and 3 layers of cortical cells. The cystocarp in this species is far more densely corticate than in any other species of the group.

The carposporophyte shows a thick erect central axis from which the gonimoblast filaments arise sympodially, developing from near the base as well as from the upper part (Figs. 16, 17).

Old cystocarps often break off, leaving the basal part of their pedicel projecting from the blade. Several young procarp-forming branchlets may develop from each of these broken pedicels.

2. **Sarcomenia victoriae** Harvey ex J. Agardh 1863: 1262; 1896: 135; 1899: 145. De Toni 1900: 739; 1924: 359.

Figs. 20–42; Plate 1, Fig. 2; Plate 2, Fig. 1

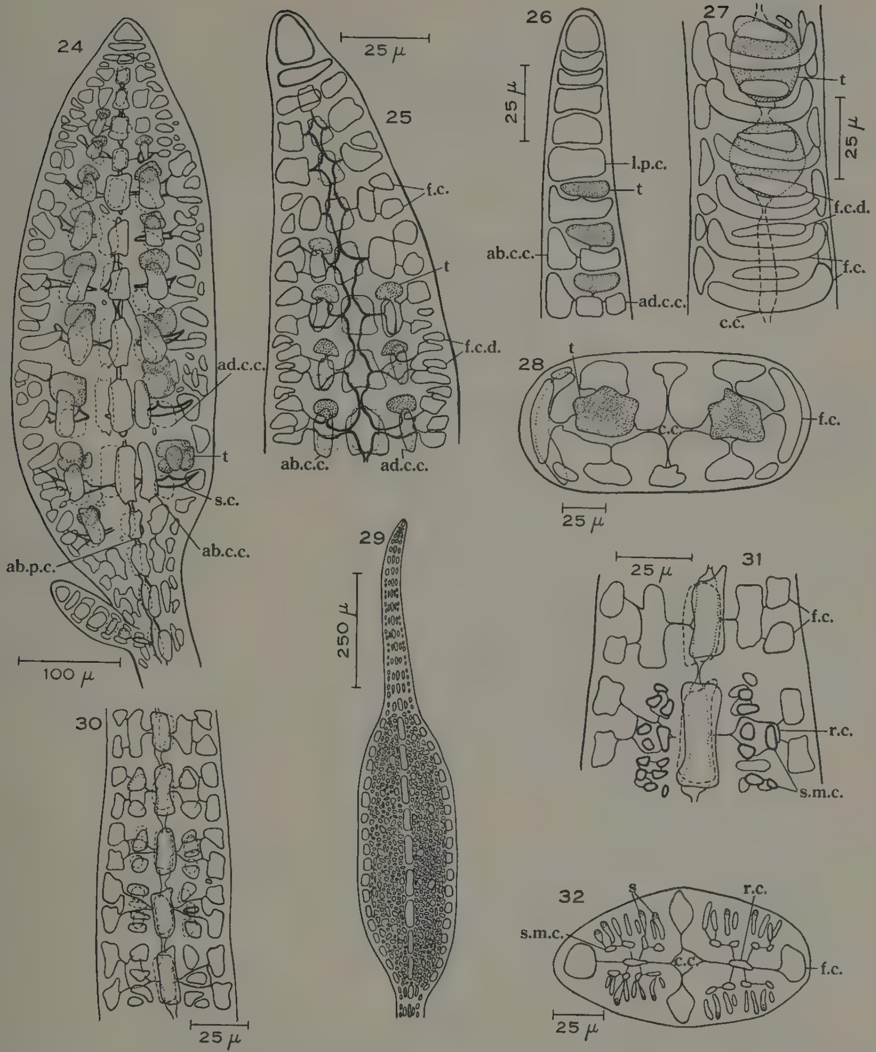
Polysiphonia victoriae Kuetzing 1864: 20, t. 56.
Sarcomenia dasyoides J. Agardh 1863: 1263; 1896: 134; 1899: 141. De Toni 1900: 738; 1924: 359.
Sarcomenia opposita J. Agardh 1899: 142, 146. De Toni 1924: 359.
Sarcomenia wilsonis J. Agardh 1899: 142. De Toni 1924: 360.

Type locality.—Port Phillip, Vic. (*Harvey* 188).

Type.—In Herb. Agardh, Lund (No. 43373).

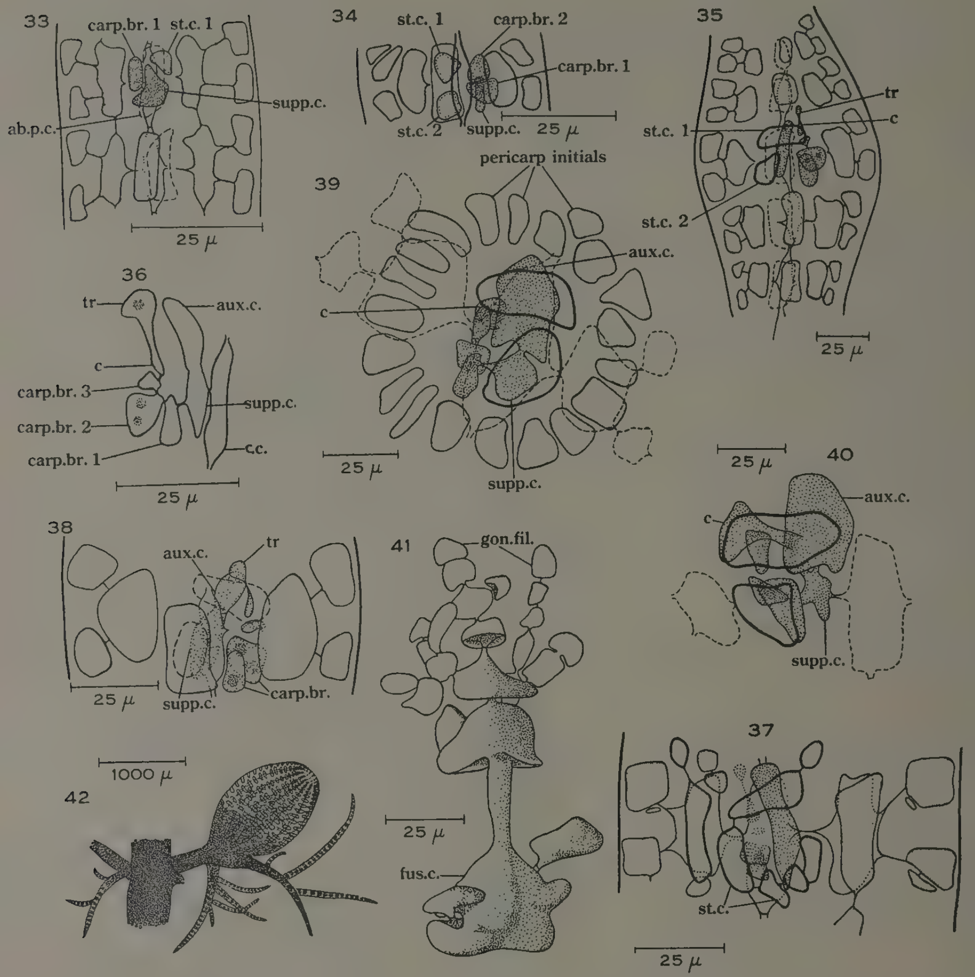
Distribution.—From Elliston, S.A., to Western Port, Vic. Sublittoral or in deeper rock platform pools on rough coasts.

Sarcomenia victoriae was first described by J. Agardh from material collected by Harvey at Port Phillip, Vic. The thallus reaches 30–35 cm in height, becoming terete in the lower regions owing to extensive cortication, while the younger branches are flattened. Branching occurs largely from the adaxial surface of the blades and is rather irregular (Plate 1, Fig. 2). The tetraspores and spermatia both develop


24
25 μ
25
26
25 μ
27
25 μ
t
l.p.c.
t
ab.c.c.
ad.c.c.
f.c.d.
f.c.
c.c.
f.c.
t
f.c.d.
ad.c.c.
ab.c.c.
ad.c.c.
t
s.c.
ab.c.c.
ab.p.c.
100 μ
28
t
c.c.
f.c.
25 μ
29
250 μ
31
25 μ
f.c.
r.c.
s.m.c.
30
25 μ
32
s
r.c.
s.m.c.
c.c.
f.c.
25 μ

Figs. 24–32.—*Sarcomenia victoriae.* Fig. 24.—Mature stichidium from the abaxial side. Fig. 25.—Tip of a stichidium, showing formation of tetrasporangia and cover cells. Fig. 26.—Longitudinal optical view of a young stichidium, mostly through the lateral pericentral cells, showing the development of the tetrasporangium and cover cells. Fig. 27.—Edge view of a stichidium, showing the curved flanking cells and their derivatives. Fig. 28.—Transverse section of a stichidium. Fig. 29.—A mature spermatangial blade. Figs. 30, 31.—Stages in the development of spermatangial mother cells. Fig. 32.—Transverse section of a spermatangial blade.

on small lateral blades which are of determinate growth. Procarps develop near the base of young lateral branchlets, and fertilization of the carpogonium and the ensuing development of the cystocarp appear to inhibit further growth of the branch, so that the cystocarp is usually seen with a short spur at the base formed by the


33
carp.br. 1
st.c. 1
supp.c.
ab.p.c.
25 μ
34
st.c. 1
carp.br. 2
carp.br. 1
st.c. 2
supp.c.
25 μ
35
tr
c
st.c. 1
st.c. 2
25 μ
pericarp initials
39
aux.c.
c
supp.c.
25 μ
36
tr
aux.c.
c
carp.br. 3
carp.br. 2
carp.br. 1
supp.c.
c.c.
25 μ
40
aux.c.
c
supp.c.
25 μ
38
aux.c.
tr
carp.br.
supp.c.
25 μ
41
gon.fil.
fus.c.
25 μ
37
st.c.
25 μ
1000 μ
42

Figs. 33–42.—*Sarcomenia victoriae*. Fig. 33.—Part of thallus, showing the first sterile cell, carpogonial branch initial, and supporting cell. Fig. 34.—The same, with 2 sterile cells and 2-celled carpogonial branch. Fig. 35.—Thallus with mature carpogonial branch and sterile cells. Fig. 36.—Side view of carpogonial branch, immediately after fertilization, with the supporting cell cutting off the auxiliary cell. Fig. 37.—Division of sterile cells and degeneration of unfertilized carpogonium. Fig. 38.—Formation of auxiliary cell from supporting cell. Fig. 39.—Fusion of carpogonium and auxiliary cell, surrounded by a ring of pericarp initials. Fig. 40.—Fusion of carpogonium and auxiliary cell by a tubular connection. Fig. 41.—A young carposporophyte, showing production of gonimoblast filaments from the erect fusion cell. Fig. 42.—Mature cystocarp.

branch from which it originally arose. At times short lateral branches occur on this spur (Fig. 42).

The thallus when fresh has a greyish iridescence. On exposure or drying it turns a rosy red and disintegrates very rapidly.

It has been impossible to find any real distinction between *S. victoriae* (Plate 1, Fig. 2) and *S. dasyoides* J. Agardh (Plate 2, Fig. 1) apart from rather more regular branching in the former and a more luxurious development of these branches. These differences seem readily accounted for as of environmental nature, where the more sparse, stunted *S. dasyoides* form comes from reef growth in rougher water and the *S. victoriae* form from more sheltered growth in bays or deeper and calmer water. This is supported by the localities from which the specimens seen have been recorded.

The type specimen of *S. opposita* J. Agardh (LD: No. 43381) is a reef form showing slightly more prominent opposite branching than usual, and *S. wilsonis* J. Agardh (LD: No. 43406) also appears to be only a form of *S. victoriae*.

Harvey distributed *S. dasyoides* and also *S. corymbosa* J. Agardh under the former name. The type of *S. dasyoides* (a Harvey specimen) is in Herb. Agardh (LD: No. 43398), but Harvey's 143E in MEL is *S. corymbosa*. J. Agardh (1863, p. 1264) also remarks on this confusion among the specimens of *S. dasyoides* distributed by Harvey. *S. victoriae* and *S. dasyoides* were both first described by J. Agardh (1863) in the same publication. As there is this confusion in Harvey's specimens of *S. dasyoides*, it is proposed to retain the name *S. victoriae*, relegating *S. dasyoides* to synonomy.

This investigation is based largely on material collected at Elliston on the west coast of Eyre Peninsula, S.A. These plants were growing under rough conditions in upper sublittoral reef pools and are of the more sparsely branched reef form of this species (= *S. dasyoides*). Cystocarpic, spermatangial, and tetrasporangial plants were all collected at the same time, in February 1954 (AD: A13518).

Structure of thallus

Growth is initiated by a single apical cell, which divides by transverse walls concave to the apex to form saucer-shaped cells (Fig. 20). The number of such cells present depends on the rate of growth at any one time. The abaxial pericentral cell is first formed, then the 2 lateral pericentral cells, and finally the adaxial pericentral cell, leaving the central cell (Figs. 20, 21). Each of the lateral pericentral cells cuts off a small cell at its anterior outer edge and later a similar cell is cut off posteriorly. These flanking cells elongate until each is about half as long as the lateral pericentral cell from which it was derived (Fig. 20). Further changes are produced only by the enlargement of the existing cells and by their cortication. Secondary pit connections develop between adjacent pericentral cells (Fig. 23) and these connections are later found more generally throughout the older blade. Lateral branches develop endogenously (Fig. 23). A single cell is cut off from the anterior end of a central cell and this acts as an apical initial, emerging anteriorly to the transverse pericentral cell and developing to form a lateral branch as described above. These lateral initials form only from the anterior end of any central cell.

Cortication of the thallus does not occur until several lateral branches have been initiated, but then follows rapidly and does not appear to follow a very definite pattern—being brought about by numerous periclinal divisions of all pericentral cells and the flanking cells (Fig. 22). The first divisions always occur in the transverse pericentral cells, usually in the vicinity of a lateral branch, and owing to more intense cortication about the transverse pericentral cells the branch becomes almost terete. Both primary and corticated branches show strong regeneration after damage or breaking.

Development of stichidia and tetrasporangia

The stichidia are formed in dense masses in the position of lateral branches. Development of stichidia follows the same pattern as that of lateral branches. Tetrasporangia develop in each stichidium in 2 regular longitudinal rows. The tetrasporangium and 2 cover cells are cut off from the lateral pericentral cells in rapid succession (Figs. 24, 25), so that the order of their formation can only be seen in young actively growing stichidia. At about the sixth or seventh segment from the tip, the tetrasporangium is cut off by an oblique wall, leaving an upturned tip to the remaining cell (Fig. 26). The abaxial cover cell, which includes this upturned tip, is next cut off, thus protecting the sporangium on the dorsal side of the stichidium. The adaxial cover cell is last formed (Fig. 26). In most cases the adaxial cover cell is only about half the length of the abaxial cover cell and situated posteriorly to the young sporangium, thus leaving the tetrasporangium at least partially exposed. The remaining part of the lateral pericentral cell, now the stalk cell, remains very thin but is nevertheless conspicuous in the stichidium (Fig. 24). Tetrasporangia develop in acropetal succession. While tetrasporangia are still being formed at the tip of the stichidium, gaps occur near the base, from which mature tetraspores have been liberated. After the liberation of the tetrahedrally arranged tetraspores, the cover cells undergo division to form groups of about 6–7 small cells to fill the gap left by the tetraspores. During the development of the tetrasporangia the flanking cells divide further, each cutting off a small cell at its anterior edge (Fig. 25). The original flanking cells, although narrow, are very extended horizontally and curved (Figs. 27, 28), thus forming a protective framework round the edges of the stichidium, while the flanking cell derivatives are far less extended and lie centrally with regard to the flanking cells, i.e. actually at the edge of the stichidium (Fig. 27).

Development of spermatangial blades

Spermatangia develop in small lateral branches similar in size to the stichidia (Fig. 29). The spermatangial blades have a distinctive appearance since only the lateral pericentral cells are fertile. Thus each spermatangial blade in surface view shows a distinct "midrib" (the transverse pericentral cells) and margin (the flanking cells) of undivided cells. The production of spermatangial mother cells from the lateral pericentral cells does not occur until about the 16th–18th segment from the apex of the blade, leaving a sterile awn at the end of each spermatangial blade. This gives quite a distinctive appearance and appears to be typical of the species (Fig. 29).

Each lateral pericentral cell first cuts off by obliquely periclinal walls 2–4 cortical cells on each side of the blade (Figs. 30, 31). These then divide anticlinally to form ultimately a group of about 16 cells—the spermatangial mother cells—lying in the surface plane. When only 2 cortical cells are formed from 1 pericentral cell, these first divide to form a row of 4, then each of these forms a row of 4 cells all lying in the same plane. If more than 2 cortical cells are formed, the development of the group of spermatangial mother cells is more irregular. The much attenuated remains of the lateral pericentral cell is visible in the median plane of spermatangial branches. Each of the spermatangial mother cells cuts off 3–4 elongate spermatangia with dense protoplasmic contents from which rounded spermatia are budded off (Fig. 32).

Development of procarp

Carpogonial branches develop only from the adaxial pericentral cells, near the base of young blades. Only 1 cystocarp develops in each branch, although occasionally 2 or even 3 young carpogonial branches may be seen in 1 blade. A cell is cut off the anterior end of the fertile adaxial pericentral cell by an oblique wall. This is the first sterile cell (Fig. 33), which comes to lie horizontally across the anterior part of the pericentral cell (Fig. 35). Next the ventral pericentral cell cuts off, laterally, the carpogonial branch initial (Fig. 33). By the time 2 cells of the carpogonial branch have been formed, the second sterile cell has been cut off from the adaxial pericentral cell and lies laterally to this on the opposite side to the carpogonial branch (Fig. 34). Thus the remainder of the adaxial pericentral cell functions as the supporting cell of the carpogonial branch.

A mature carpogonial branch is 4-celled, with the carpogonium surmounted by a short trichogyne with a broad, expanded tip (Figs. 35, 36). Of this 4-celled carpogonial branch the second cell is the largest and is frequently seen to be binucleate (Fig. 36). The larger second cell also lies nearer the adaxial surface of the blade than the other cells of the carpogonial branch, which all lie in the same plane. The large second cell of the carpogonial branch thus occupies the space between the 2 sterile cells on the ventral surface of the blade. The third cell of the carpogonial branch is the smallest. The carpogonium and trichogyne in all cases point towards the tip of the branch.

If fertilization fails to take place the 2 sterile cells divide further and the carpogonial branch disintegrates (Fig. 37). These sterile cell derivatives are the start of cortication of the branch.

Development of cystocarp

Following fertilization of the carpogonium, the anterior end of the supporting cell enlarges and is cut off to form the auxiliary cell (Figs. 38, 39), with which the enlarging carpogonium comes to lie in close proximity. A short tube forms between the carpogonium and this auxiliary cell (Figs. 39, 40) and the carpogonial branch soon begins to disintegrate. Fusions occur between the supporting cell, auxiliary cell, and central cell to form a large, irregular fusion cell, from which an erect prolongation develops (Fig. 41). From this arise numerous much-branched gonimoblast filaments which ultimately develop terminal oval carposporangia which are 80–100 μ in length and densely cytoplasmic. The cytoplasmic connections between the fusion cell and the lower cells of the carposporophyte become very much enlarged and a massive column is formed from which the gonimoblast filaments arise (Fig. 41). The upper cells of this column are characteristically umbrella-shaped. The 2 sterile cells undergo no further development, and following fertilization they appear to disintegrate.

Following fertilization of the carpogonium and formation of the auxiliary cell, the development of the protective pericarp is initiated by the lateral pericentral cells and flanking cells of the fertile segment and the adaxial pericentral cells of the segments anterior and posterior to the fertile one (Fig. 39). From these cells are formed a ring of vertical chains of cells, which surround the developing carposporophyte. Each of the cells of these vertical chains cuts off, one above the other, 2 laterally elongate cells on the outside, so that the cystocarp has a double wall of cells. Cells of the adjacent outer rows usually alternate. Secondary pit connections develop between the horizontal outer cells but not between the vertical rows of cells. The globose pericarp opens at the apex by a small circular ostiole, through which the mature carpospores are liberated (Fig. 42). The cystocarp increases greatly in size, reaching 800–1000 μ in width and 900–1400 μ in length, by enlargement of the cells and their separation during growth. As the cystocarp matures, cortication of the basal portion occurs along with cortication of the parent branch.

3. **Sarcomenia corymbosa** J. Agardh 1896: 134. De Toni 1900: 737; 1924: 359.

Figs. 43–50; Plate 2, Fig. 2

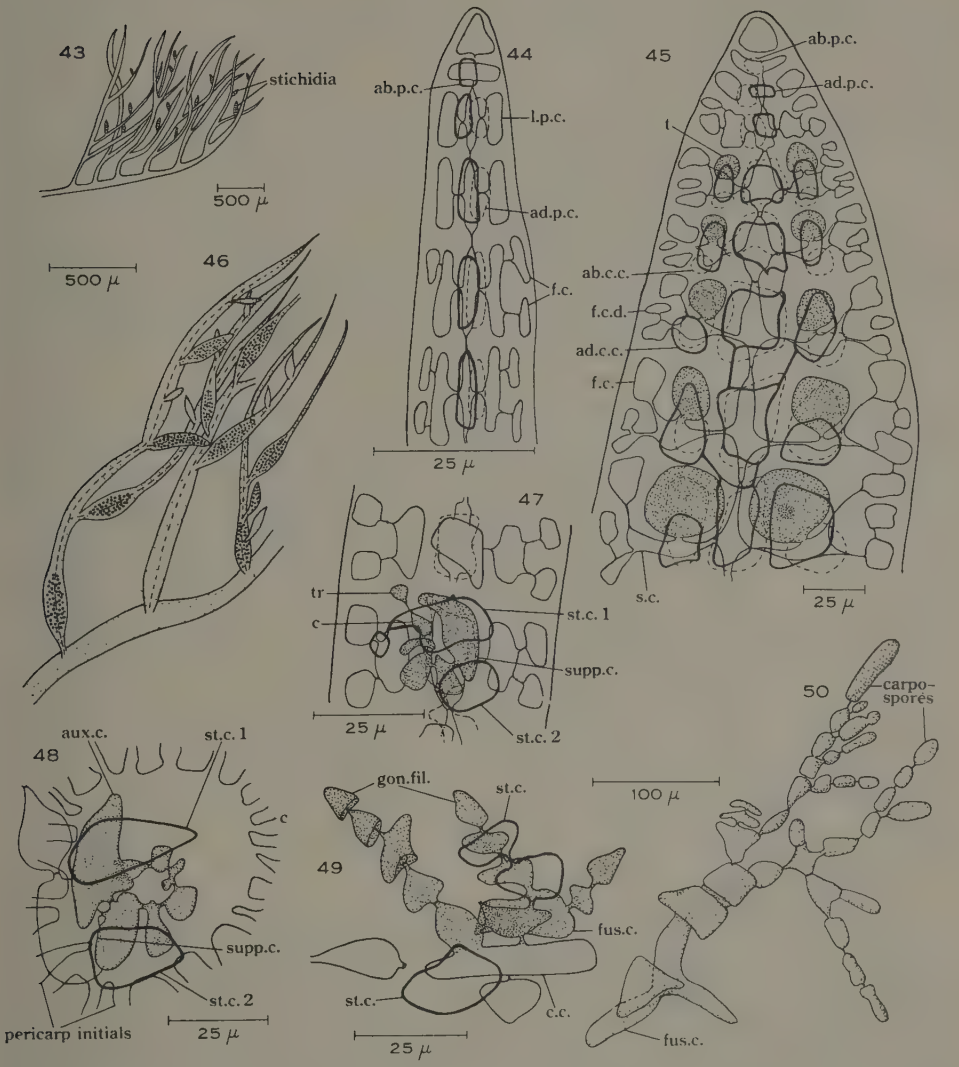
Type locality.—Western Port, Vic. (*J. B. Wilson* No. 41).

Type.—Herb. Agardh, Lund (No. 43355).

Distribution.—From Sturt Bay, S.A., to Phillip I., Vic., and the north coast of Tasmania. Sublittoral on rough coasts.

The thallus of this species reaches a height of about 30 cm. The main branches are generally alternate, while the tips of the branches show very distinct unilateral branching (Plate 2, Fig. 2). Branching is largely from the adaxial surface of the parent branch. Owing to this and to the density of branching in the younger parts of the thallus, the top of the plant tends to be flat or corymbose in form. When the plant is undergoing rapid vegetative growth all of these upper unilateral branches are uncorticate. Fertile specimens show a greater degree of cortication in these upper branches, although even then the younger branches are not corticate. There has been some confusion between *S. victoriae* and *S. corymbosa*, but study of the types of both species and a range of specimens shows the following distinctions.

S. victoriae has basically opposite branching, often with long lateral branches from near the base of the plant. Lesser branches are pinnately arranged and the plant is densely corticate except for the ultimate branches. *S. corymbosa* has alternate branching in the older parts and the ultimate branches are distinctly unilateral, arising adaxially. Thus the upper parts of *S. corymbosa* are dense and corymbose. Branches formed near the base of the plant are often lost relatively early. In rapidly growing plants the upper branches up to the fourth and sometimes higher orders are uncorticate. The spermatangial branches of *S. victoriae* and *S. corymbosa* are also distinct, those of the former being simple and determinate while in the latter they are often branched and relatively indeterminate.


43
stichidia
500 μ
46
500 μ
44
ab.p.c.
l.p.c.
ad.p.c.
f.c.
25 μ
45
ab.p.c.
ad.p.c.
t
ab.c.c.
f.c.d.
ad.c.c.
f.c.
s.c.
25 μ
47
tr
c
st.c. 1
supp.c.
st.c. 2
25 μ
48
aux.c.
st.c. 1
c
supp.c.
st.c. 2
pericarp initials
25 μ
49
gon.fil.
st.c.
fus.c.
st.c.
c.c.
25 μ
50
carpo-
spores
100 μ
fus.c.

Figs. 43–50.—*Sarcomenia corymbosa.* Fig. 43.—Upper part of thallus with stichidia and showing unilateral branching. Fig. 44.—Branch apex, showing segmentation. Fig. 45.—Upper part of a stichidium. Fig. 46.—Branches of a male plant bearing spermatangial sori. Fig. 47.—Mature carpogonial branch and sterile cells (one of which has divided). Fig. 48.—Fusion between auxiliary cell and carpogonium, and initiation of pericarp. Fig. 49.—Fusion between auxiliary cell and central cell, and early formation of gonimoblast filaments. Fig. 50.—Upper part of a gonimoblast filament with young terminal carposporangia.

As *S. corymbosa* is very similar to *S. victoriae* in many details of its structure and development, the main features only are described. The material available permitted a detailed study of all phases of the species.

Material of *S. corymbosa* was collected at Vivonne Bay, Kangaroo I., S.A., Jan. 1946 (AD: A2855), at Port McDonnell, S.A., Aug. 1953 (AD: A18991), and Robe, S.A., Dec. 1953 (AD: A19937).

Structure of thallus

Segmentation of the apical cell, the order of development of pericentral cells and flanking cells (Fig. 44), and the development of endogenous lateral branches are the same as described for *S. victoriae.*

The basal portions of plants of *S. corymbosa* are densely corticate and become terete. Depending on the stage of growth, the upper parts of the thallus are more or less densely corticate. The corticating cells in this species tend to be rather elongate and occur in longitudinal rows, in contrast to *S. victoriae*, *S. mutabilis*, and *S. hypneoides*, where the corticating cells are rhomboidal in form.

Development of stichidia and tetrasporangia

The stichidia are always produced adaxially on the parent branches (Fig. 43) and are essentially similar in form to those already discussed in *S. victoriae.* The tetrasporangia and 2 cover cells are cut off in rapid sequence from the lateral pericentral cells, the abaxial cover cell usually being the larger, though occasionally the abaxial and adaxial cover cells alternate in size in successive segments (Fig. 45). Secondary pit connections may occur between the cover cells and transverse pericentral cells (Fig. 45). In the stichidium the posterior of the 2 flanking cells in each segment divides horizontally before the anterior one, but eventually 4 cells are formed (Fig. 45). These cells, especially the original flanking cells, elongate horizontally and form a curved protective edge around the stichidium. After the tetraspores are liberated, cell divisions occur in and around the small ventral cover cell (occasionally also around the dorsal cover cell), and the ends of the curved flanking cells may also be cut off.

Development of spermatangial blades

The spermatangial blades of *S. corymbosa* differ from those of all other species investigated. They are lateral branches of unlimited growth and the patches of spermatia occur near their base (Fig. 46). These branches continue to grow in length and also themselves produce branches which may bear spermatia. The spermatangia are formed from the 2 lateral pericentral cells. In a few cases transverse pericentral cells were seen to divide to form spermatangia, but this was exceptional. Each lateral pericentral cell cuts off a group of spermatangial mother cells on both surfaces of the blade. From each of these spermatangial mother cells 2 or 3 elongate spermatangia are formed by anticlinal divisions and spermatia are budded off from their tips.

Development of procarp

Procarps develop from the adaxial pericentral cells in lateral branches. The first sterile cell is cut off from the anterior end of the pericentral cell, followed by the carpogonial branch initial. By the time the carpogonial branch is 2-celled, a second sterile cell has been cut off from the adaxial pericentral cell, lying lateral to the pericentral cell and opposite the young carpogonial branch.

The mature carpogonial branch is 4-celled, the second cell being the largest and often showing 2 nuclei (Fig. 47). The carpogonium is surmounted by a short trichogyne with a globular tip.

Development of cystocarp

After fertilization of the carpogonium the anterior part of the supporting cell is cut off to form the auxiliary cell. The carpogonium enlarges and lies in close proximity to this cell and fusion occurs between the fertilized carpogonium and the auxiliary cell (Fig. 48). Subsequently fusions also occur between the auxiliary cell, central cell, and supporting cell (Fig. 49), forming the large basal fusion cell, from which the erect carposporophyte structure develops in an irregularly sympodial manner, producing gonimoblast filaments with terminal, ellipsoidal carposporangia (Fig. 50).

Following fertilization of the carpogonium, the pericarp is initiated and a ring of cells develops round the procarp. These cells divide to form upright chains of cells and each cuts off externally 2 more or less isodiametric cells lying horizontally. The wall of the mature, urceolate cystocarp thus consists of 2 distinct cell layers. Corticating cells develop in the basal part of the cystocarp when cortication of the supporting branch occurs.

4. **Sarcomenia hypneoides** Harvey 1854: 537; 1858: pl. 12. J. Agardh 1863: 1266; 1896: 137; 1899: 143. De Toni 1900: 741; 1924: 360.

Figs. 51–54; Plate 3, Fig. 1

Type locality.—"Fremantle and Garden Island", W.A. (*Harvey* 142)

Type.—In Herb. Harvey (TCD) No. 142A.

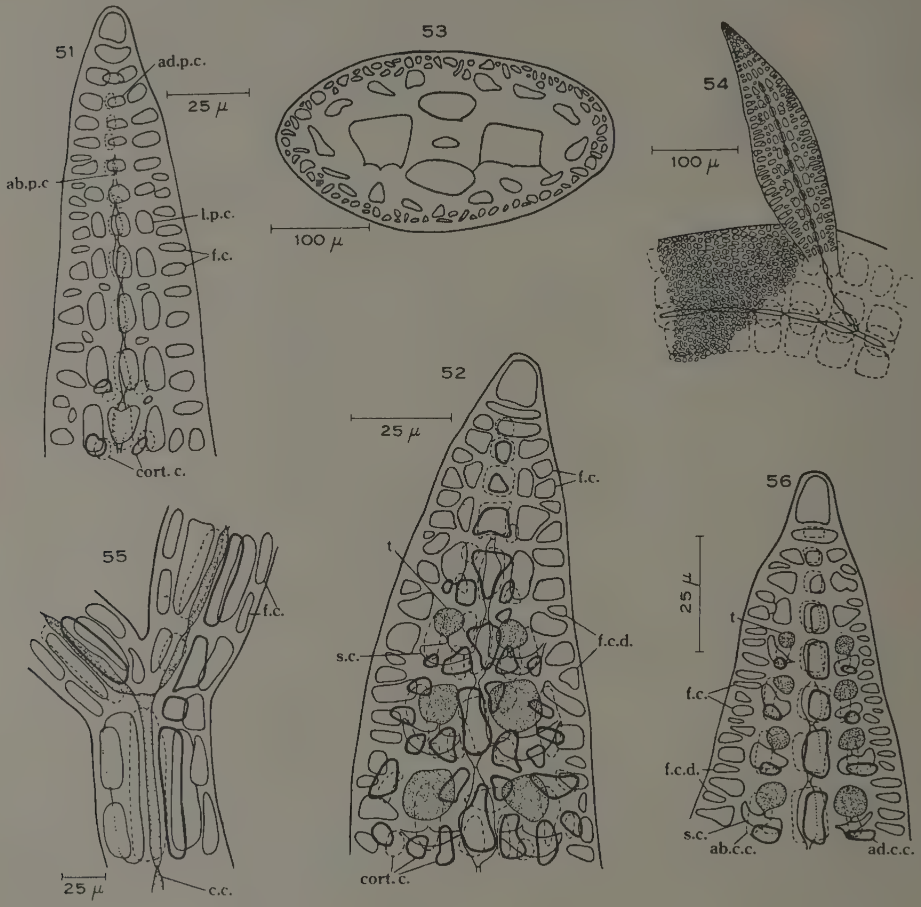
Distribution.—Only known from Fremantle and Garden I., W.A. Apparently rare.

This species has been studied from dried herbarium specimens only (AD: A18446, A18301) collected near Fremantle by Harvey and G. Clifton. The thallus, which reaches a height of about 20 cm, shows opposite branching in most parts. In one specimen (Plate 3, Fig. 1) the ends of several branches had become curled in a tendril-like manner—similar to those found in some specimens of *S. delesserioides*. The thallus is basically like *S. victoriae* in structure, differing principally in the greater degree of cortication, which produces a coarser plant.

Structure of thallus

Growth is initiated by a hemispherical apical cell, which cuts off segments by transverse walls (Fig. 51). Each of these subapical cells very soon develops 4 pericentral cells, the abaxial pericentral cell being formed first. This is followed by the 2 lateral pericentral cells and lastly by the adaxial pericentral cell. Each of the lateral pericentral cells cuts off 2 flanking cells towards the edge of the blade (Fig. 51).

Lateral branches arise endogenously from the anterior end of a central cell. The lower segments of lateral branches are immersed in the thick thallus and the basal 6 segments or so do not develop pericentral cells or flanking cells. A chain of central cells may be seen between the lateral branch and the central cell of the parent branch (Fig. 54). Cortication occurs very rapidly following branch initiation, leaving only the growing tips ecorticate (Fig. 51). Cortical cells are cut off first by the abaxial pericentral cells and this is followed by divisions of the adaxial pericentral cells and later the lateral pericentral cells and flanking cells. All the branches become covered by several layers of small corticating cells (Figs. 53, 54), which are rhomboidal in shape, similar to those of *S. victoriae*. The branches remain slightly flattened even when fully corticate. Prominent secondary pit connections are visible between the pericentral and flanking cells. Secondary connections are also visible between the corticating cells.



Figs. 51–54.—*Sarcomenia hypneoides*. Fig. 51.—Apex of branch, showing segmentation and early cortication. Fig. 52.—Apex of a stichidium, showing early cortication. Fig. 53.—Transverse section of a branch. Fig. 54.—Young lateral branch. Figs. 55, 56.—*Sarcomenia mutabilis*. Fig. 55.—Departure of a lateral branch. Fig. 56.—Apex of a stichidium.

Development of stichidia and tetrasporangia

The stichidia (Fig. 52) are similar in form to those of *S. victoriae.* The tetrasporangia are produced from the lateral pericentral cells and 2 cover cells are cut off almost simultaneously. The cover cell formed on the adaxial surface of the blade is generally only half the length of the abaxial cover cell, which is equal to the transverse pericentral cell in length. Each flanking cell in the stichidium divides horizontally into two. Cortication of the stichidium commences even before the formation of the tetrasporangia and cover cells (Fig. 52), cells being cut off from both transverse pericentral cells. After the tetraspores have been liberated, the adaxial cover cell divides further, merging with the general cortication. As in the vegetative thallus, the stichidium of *S. hypneoides* is more heavily corticated than in other species.

5. **Sarcomenia mutabilis** (Harvey) J. Agardh 1863: 1261; 1896: 134. De Toni 1900: 736; 1924: 359.

Figs. 55, 56; Plate 3, Fig. 2

Polysiphonia mutabilis Harvey 1854: 540. Kuetzing 1864: 20, t. 55*d–g*.

Type locality.—Fremantle, W.A. (on *Zostera*).

Type.—In Herb. Harvey (TCD) No. 116A. *Isotype.*—AD: A18300.

Distribution.—From Fremantle, W.A., to Port Stephens, N.S.W., and Low Head, Tas. Sublittoral, not common.

Sarcomenia mutabilis was available for study only from dried herbarium specimens. Isotype material (AD: A18300) was used for the most part, but other specimens were also studied. Stichidia were present on the isotype material. The thallus is of delicate form and usually 4–10 cm in height (Plate 3, Fig. 2). The size, form, and slight degree of cortication satisfactorily separate *S. mutabilis* from all other species of the group.

Structure of the thallus

As in the other species of the *Sarcomenia* group already discussed, growth is initiated by a hemispherical apical cell (Fig. 56). The cells cut off by horizontal divisions each produce 4 pericentral cells. The abaxial pericentral cell is formed first, followed by the lateral pericentral cells and finally the adaxial pericentral cell. Each lateral pericentral then cuts off 2 flanking cells, giving a flattened branch 5 cells wide and 3 cells thick in the centre. The statement of Silva and Cleary (1954, p. 259) that flanking cells are lacking in *S. mutabilis* is based on a misidentification of *Polysiphonia roeana* (see below).

Branching is endogenous (Fig. 55), originating from the anterior end of a central cell. The basal segment of a lateral branch often lacks flanking cells.

Cortication is slight and only becomes complete in the lower branches of the thallus. The corticating cells are small and generally rhomboidal in outline, similar to those formed in *S. victoriae*.

Development of stichidia and tetrasporangia

The stichidia are similar in shape and development to those of *S. victoriae.* The tetrasporangia are derived from the lateral pericentral cells, which also cut off 2 cover cells (Fig. 56). The adaxial cover cell is only half the length of the abaxial cover cell, which approximately equals the transverse pericentral cells in length. Each flanking cell divides horizontally into two. The mature tetraspores are arranged tetrahedrally in the tetrasporangium.

6. **Sarcomenia tenera** (Harvey) J. Agardh 1863: 1264; 1896: 136; 1899: 145. De Toni 1900: 740; 1924: 360.

Figs. 57–71; Plate 4, Fig. 1

Dasya tenera Harvey 1854: 543; 1863: pl. 257. Kuetzing 1865: 1, t. 1*c–d*, t. 2.
Sarcomenia secundata J. Agardh 1899: 147. De Toni 1924: 361.

Type locality.—Fremantle, W.A. (*Harvey*).

Type.—In Herb. Harvey (TCD), No. 78 in travelling set.

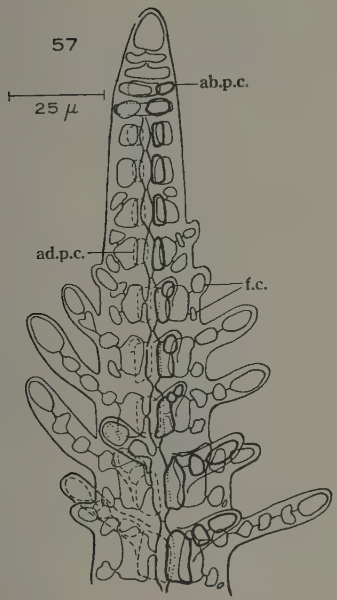
Distribution.—From Fremantle, W.A., to Western Port, Vic., and the north coast of Tasmania. Sublittoral.

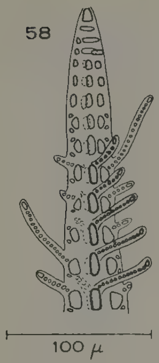
Plants of *S. tenera* reach a height of 30 cm. The degree of cortication is such that only the young branches show flattening and the greater part of the thallus is terete. Branching is irregular and, in some older plants, sparse (Plate 4, Fig. 1). The growing apices bear monosiphonous filaments which are produced both from the flanking cells and the transverse pericentral cells and give a villose appearance just visible to the naked eye. Cells of these filaments contain numerous chromatophores. The thallus when fresh has a greyish red iridescence, but on exposure or when confined in limited water the thallus becomes a bright rosy red and rapidly disintegrates. The material for this investigation was collected as drift at Marion Bay, Yorke Peninsula, S.A., in April 1950 (AD: A16097).

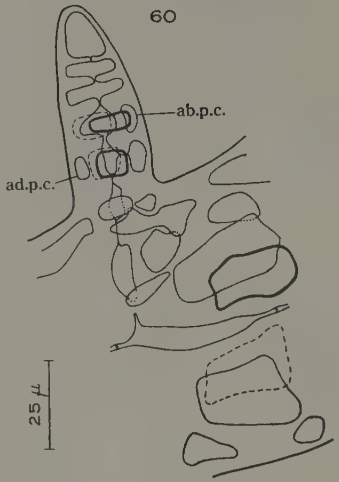
The type of *S. secundata* J. Agardh (LD: No. 43459) appears to be identical with *S. tenera.* The other specimen of J. Agardh from Waterloo Bay (*O'Halloran*) is, however, *S. victoriae.*

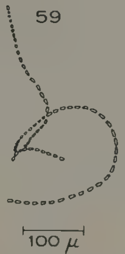
Structure of thallus

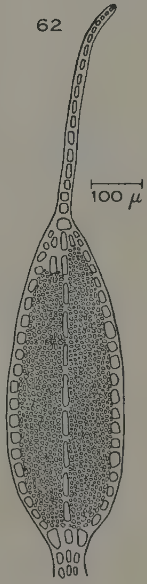
The apical region and development of pericentral cells is similar to that described for other species, i.e. the abaxial pericentral cell is first formed, followed by the 2 lateral pericentral cells and lastly by the adaxial pericentral cell (Fig. 57). A small cell is cut off by an oblique wall at the anterior outer edge of each lateral pericentral cell, and later a similar cell is formed at the posterior outer edge. Thus 2 flanking cells are formed by each lateral pericentral cell (Figs. 57, 58). The anterior member of each pair of flanking cells develops further to form a monosiphonous filament up to 25 cells long. Similar monosiphonous filaments are formed from the anterior ends of both transverse pericentral cells (Figs. 57, 58), slightly further from the branch apex. The terminal cell of each filament is oval and measures about 10 by 7 μ. On older branches these filaments usually branch, often 2 or 3 times (Fig. 59), but soon fall off. They occur very prolifically on the growing tips of the

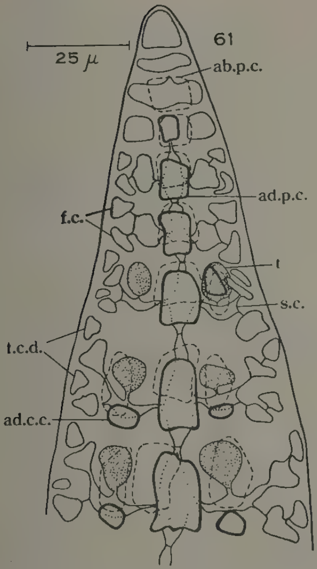

57
25 μ
ab.p.c.
ad.p.c.
f.c.

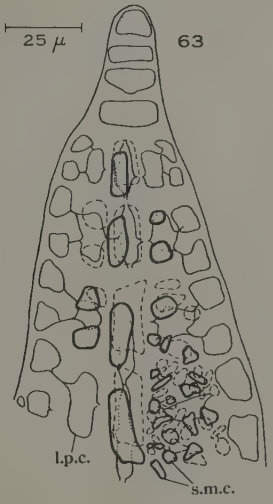



60
ab.p.c.
ad.p.c.
25 μ






25 μ
61
ab.p.c.
ad.p.c.
f.c.
t
s.c.
t.c.d.
ad.c.c.


25 μ
63
l.p.c.
s.m.c.

Figs. 57–63.—*Sarcomenia tenera*. Fig. 57.—Branch apex, showing segmentation and development of monosiphonous filaments. Fig. 58.—Branch apex, further developed than in Fig. 57. Fig. 59.—A branched monosiphonous filament. Fig. 60.—Origin of a lateral branch. Fig. 61.—Apex of a stichidium, adaxial view. Fig. 62.—A mature spermatangial blade. Fig. 63.—Apex of a young spermatangial blade, showing development of spermatangial mother cells.

branches, become more scattered away from the tip, and are usually entirely absent from older branches.

Lateral branches develop endogenously from the anterior end of a central cell (Fig. 60), similarly to previously described species. Cortication commences relatively early in *S. tenera* (usually at about the 15th–18th segment) and only the young growing tips are uncorticate. Corticating cells are first cut off from the transverse pericentral cells, then from the lateral pericentral cells and flanking cells, until the branch becomes completely corticate and terete. A greater degree of cortication occurs in this species than in *S. victoriae*.

Development of stichidia and tetrasporangia

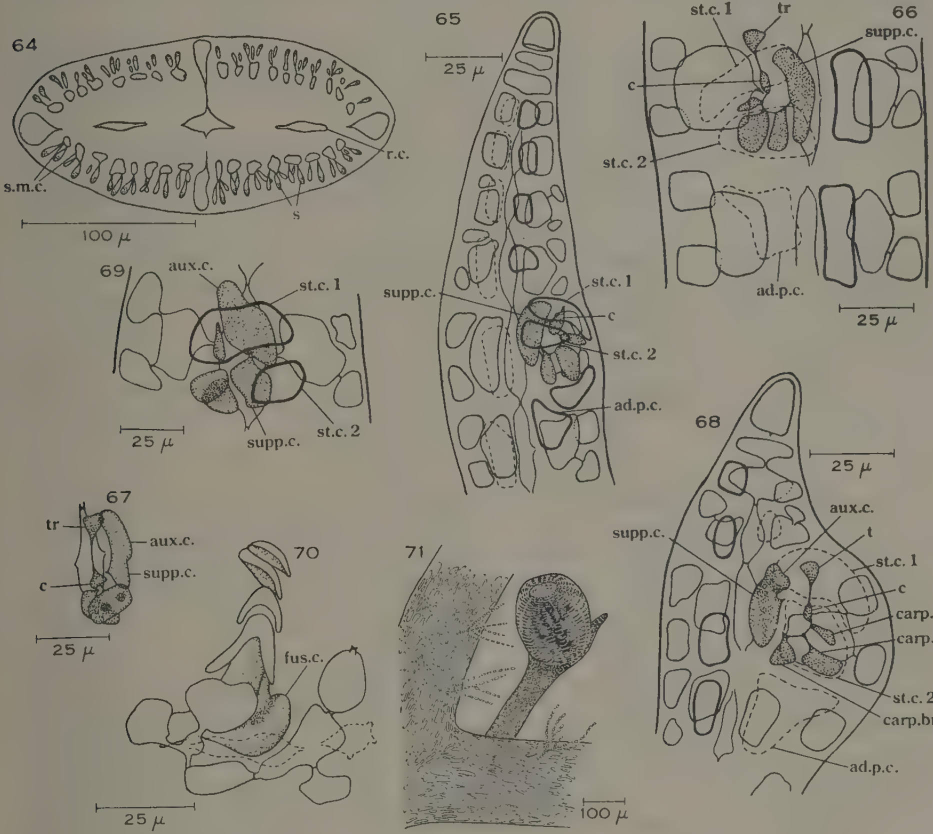
Solitary stichidia are produced laterally from mature corticated branches, mainly from the adaxial surface. The stichidia develop similarly to lateral branches (Fig. 61). Each of the flanking cells cuts off a small cell anteriorly and these flanking cells become horizontally elongate and curved, forming a protective edge to the stichidium. The lateral pericentral cells of the stichidium cut off the tetrasporangium, abaxial cover cell, and adaxial cover cell in rapid succession as in other species of the *Sarcomenia* group and the sporangium is partly exposed on the adaxial side of the stichidium. Following the liberation of the tetrahedrally arranged tetraspores, the cover cells undergo further division and the stichidium becomes progressively corticate from the base.

Development of spermatangial blades

Small spermatangial blades are formed in groups on the main branches. They develop as normal lateral branches, and spermatangial mother cells are formed by anticlinal division of cortical cells cut off from the lateral pericentral cells (Figs. 62, 63). More spermatangial mother cells (16–32) are produced from each lateral pericentral cell in this species than in other species of the group. In a transverse section of the spermatia-producing blade (Fig. 64) about 8 spermatangial mother cells correspond to each lateral pericentral cell, compared to about 4 in the previously discussed species of *Sarcomenia*. Initiation of divisions producing spermatangial mother cells appears to depress formation of pericentral cells and flanking cells, so that each spermatia-producing blade is surmounted by a long monosiphonous awn (Fig. 62).

Development of procarp

Initiation of the procarp occurs near the tip, usually in about the fifth to eighth segment, of a lateral branch (Fig. 65). Owing to this position of procarp initiation the mature cystocarp is borne on a longer “stalk” than in some other species (e.g. *S. victoriae*), where procarp initiation occurs nearer the base of the fertile lateral branch. In each fertile lateral branch usually only one procarp is initiated. The first sterile cell is cut off at the anterior end of the fertile adaxial pericentral cell. A cell is then cut off laterally by the pericentral cell and this acts as initial for the 4-celled carpogonial branch. A second sterile cell is next cut off and lies over the carpogonial branch. The remainder of the adaxial pericentral cell acts as the supporting cell of the carpogonial branch (Figs. 65, 66). The 4-celled carpogonial branch is surmounted by a short trichogyne with a very prominent tip (Fig. 66) and the second cell of the carpogonial branch is the largest and frequently binucleate. In *S. tenera* additional protection is given to the developing procarp by the adaxial pericentral cell of the next posterior segment, which acts as an extra "cover cell". This pericentral cell may itself extend toward the procarp (Figs. 66, 68) or it may cut off an additional cell which performs this protective function (Fig. 65). If fertilization fails to occur, the sterile cells divide and initiate cortication in the region of the procarp.


64
s.m.c.
r.c.
s
100 μ
65
25 μ
supp.c.
st.c. 1
c
st.c. 2
ad.p.c.
st.c. 1
tr
66
supp.c.
c
st.c. 2
ad.p.c.
25 μ
69
aux.c.
st.c. 1
25 μ
supp.c.
st.c. 2
68
25 μ
aux.c.
t
supp.c.
st.c. 1
c
carp.br. 3
carp.br. 2
st.c. 2
carp.br. 1
ad.p.c.
67
tr
aux.c.
supp.c.
c
25 μ
70
fus.c.
25 μ
71
100 μ

Figs. 64–71.—*Sarcomenia tenera.* Fig. 64.—Transverse section of a spermatangial blade. Figs. 65, 66.—Mature carpogonial branches, with 2 sterile cells and protection also from a derivative of the adaxial pericentral cell of the posterior segment. Figs. 67, 68.—Division of the supporting cell to cut off the auxiliary cell after fertilization. Fig. 69.—Auxiliary cell with old carpogonial branch. Fig. 70.—Formation of "capping cells" from the erect fusion cell. Fig. 71.—A mature cystocarp.

Development of cystocarp

After fertilization the auxiliary cell is cut off from the anterior portion of the supporting cell (Figs. 67, 69). The fertilized carpogonium increases in size and comes to lie nearer the enlarging auxiliary cell. Fusion occurs between these 2 cells by means of a short fusion tube and a binucleate cell is formed. This cell enlarges considerably and produces large "capping cells" connected by wide pit connections (Fig. 70). Fusions occur between auxiliary cell, supporting cell, and central cell to form the large fusion cell from which the vertical structure of capping cells arises. Repeated sympodial branching of this structure produces numerous gonimoblast filaments, each of which terminates in a large ellipsoidal carposporangium.

The developing carposporophyte is surrounded by a protective pericarp which is initiated only after fertilization of the carpogonium has occurred. The adaxial pericentral cells anterior and posterior to the fertile segment, the lateral pericentral cells, and the flanking cells all take part in the production of the pericarp. A complete ring of cells is formed which grows up around the developing carposporophyte. Each cell of the ring produces a vertical chain of cells, from each of which, except the apical cell, 2 cells are cut off externally, one above the other, lying horizontally across the inner row of cells. Thus the protective pericarp is made up of 2 layers of cells (Fig. 71).

7. **Sarcomenia dolichocystidea** J. Agardh 1896: 135; 1899: 145. De Toni 1900: 740; 1924: 361.

Figs. 72–82; Plate 4, Fig. 2

Type locality.—Brighton Beach, Port Phillip, Vic. (*Harvey* 209F).

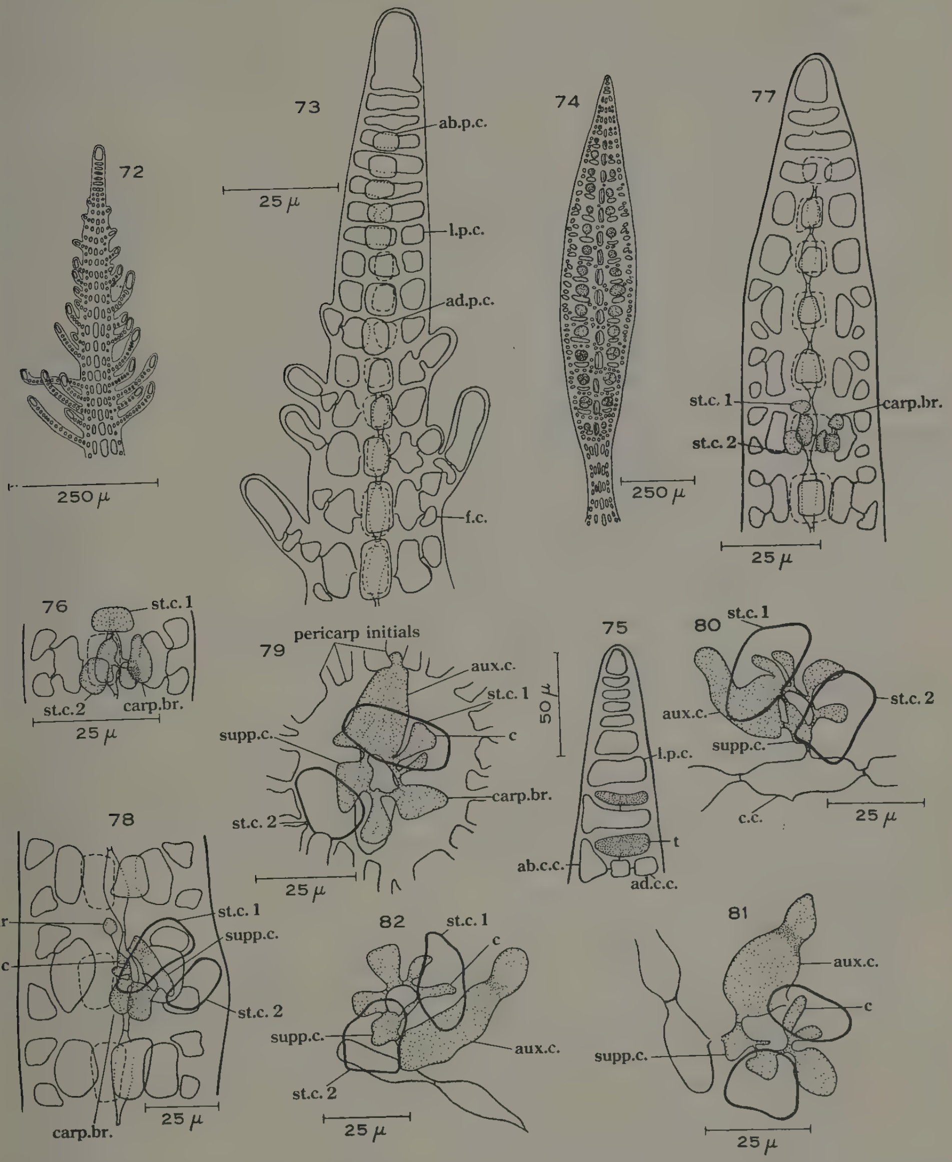
Type.—In Herb. Agardh, Lund (No. 43444).

Distribution.—From King George's Sound, W.A., to Port Phillip, Vic., and at Gordon, Tas. Usually found in relatively sheltered places, sublittoral.

This species is similar to *S. tenera* but is of more slender form and in general smaller at maturity (Plate 4, Fig. 2). Cortication is dense and only the young growing tips are uncorticate. The older parts of the thallus are terete. The apices of the branches are densely clothed with monosiphonous filaments which give a distinctive appearance to the species (Fig. 72). These monosiphonous filaments contain numerous chromatophores and may branch on older parts of the thallus, frequently each filament having 3 branches. The filaments are sparse away from the actual growing tip and finally in older parts of the thallus they are lost altogether. As with other species of the *Sarcomenia* group, *S. dolichocystidea* on exposure or when confined in a small amount of water becomes a bright rosy red and rapidly disintegrates. The material used in this investigation was collected in August 1954 at American River Inlet, Kangaroo I., S.A. (AD: A19788).

Structure of the thallus

In cell structure and cell formation *S. dolichocystidea* differs from *S. tenera* only in the position of the monosiphonous filaments. Only the upper of each pair of flanking cells produces filaments, i.e. the filaments are formed only laterally (Figs. 72, 73). At first the filaments tend to be formed on alternate sides in successive segments, but later they form on both sides of the same segment. The filaments themselves are rather coarser than those of *S. tenera*, this being especially evident in the terminal cell of the filament, which is here much longer and somewhat broader,


72
250 μ
73
ab.p.c.
25 μ
l.p.c.
ad.p.c.
f.c.
74
250 μ
77
st.c. 1
carp.br.
st.c. 2
25 μ
76
st.c. 1
st.c. 2
carp.br.
25 μ
79
pericarp initials
aux.c.
st.c. 1
supp.c.
c
carp.br.
st.c. 2
25 μ
75
50 μ
l.p.c.
t
ab.c.c.
ad.c.c.
80
st.c. 1
aux.c.
st.c. 2
supp.c.
c.c.
25 μ
78
tr
c
st.c. 1
supp.c.
st.c. 2
carp.br.
25 μ
82
st.c. 1
c
supp.c.
aux.c.
st.c. 2
25 μ
81
aux.c.
c
supp.c.
25 μ

Figs. 72–82.—*Sarcomenia dolichocystidea.* Fig. 72.—Apex of a branch, with monosiphonous filaments from the flanking cells only. Fig. 73.—Branch apex, showing segmentation and formation of monosiphonous filaments. Fig. 74.—A stichidium. Fig. 75.—Optical longitudinal view (through the lateral pericentral cells) of the apex of a stichidium, showing formation of the tetrasporangium and cover cells. Fig. 76.—A 2-celled carpogonial branch. Fig. 77.—Branch apex with a 3-celled carpogonial branch. Fig. 78.—A mature carpogonial branch. Fig. 79.—Fusion between carpogonium and auxiliary cell and initiation of pericarp. Figs. 80, 81.—Development of fusion cell. Fig. 82.—Further development of fusion cell, and a connection between carpogonium and supporting cell.

measuring on an average 20 by 8·5 μ (Fig. 72). Lateral branches are formed endogenously, as in *S. tenera* and the other species discussed previously.

Corticating cells are formed, as in *S. tenera*, on the branches quite near the growing point and although the young branches are flat the rest of the thallus is terete in form.

Development of stichidia and tetrasporangia

The stichidia in this species are rather longer than those of *S. tenera* (Fig. 74) and tend to become considerably corticated. However, the formation and development of tetraspores occur in the same manner as described for *S. tenera*, with the tetrasporangium being cut off before the cover cells (Fig. 75).

Development of spermatangial blades

Blades producing spermatia are exactly like those of *S. tenera* in structure and formation of spermatia-bearing cells. These blades have the same sterile monosiphonous awn at the tip of the spermatia-bearing tissue as in *S. tenera*.

Development of procarp and cystocarp

Formation and development of procarps follow the normal pattern previously described for other species. The fertile adaxial pericentral cell cuts off the carpogonial branch initial and 2 sterile cells, itself remaining as the supporting cell (Figs. 76, 77). The mature carpogonial branch is 4-celled and the trichogyne has a very pronounced globular tip at the end of a short, slender stalk (Fig. 78). After fertilization the supporting cell cuts off the auxiliary cell towards the tip of the branch, and the carpogonium and auxiliary cell fuse (Figs. 79–81). Also, in this species, connection has been seen between the carpogonium and the supporting cell (Fig. 82). Gonimoblast filaments develop as described previously and carposporangia are produced terminally. The structure of the pericarp is the same as in *S. tenera*, the wall of the cystocarp being composed of 2 layers of cells. The lower part of the urceolate cystocarp becomes corticated and this cortication merges with that of the branch bearing the cystocarp.

IV. OTHER TAXA ALLIED TO SARCOMENIA

1. **Platysiphonia miniata** (C. Agardh) Boergesen 1931: 1–9. Silva and Cleary 1954: 251. Cribb 1956: 187.

Figs. 83–99

Hutchinsia miniata C. Agardh 1828: 94.
Polysiphonia miniata (C. Agardh) Kuetzing 1849: 820.
Sarcomenia miniata (C. Agardh) J. Agardh 1863: 1260; 1896: 133. Weber van Bosse 1896: 281–5, t. 359. De Toni 1900: 735; 1924: 359.

Type locality.—Cadiz, Spain (*Cabrera*).

Type.—In Herb. Agardh, Lund (No. 43346).

Distribution.—From Kangaroo I., S.A., around the south-east coast of Australia to the Burnet River, Qld. Mostly sublittoral, extending into lower littoral at least on Kangaroo I. Cribb (1956: 187) has recorded *P. miniata* from Devonport, Tas. Also known from Spain, South Africa, and India.

Study of *P. miniata* was made on preserved material collected from rock platform pools at Vivonne Bay, Kangaroo I., Jan. 1950 (AD: A12914). This material has been compared with the type and agrees with it well. Individual plants are only ½–1½ cm high, and together form a turf-like mat with small coralline algae. Tetrasporic plants were abundant, spermatangial plants rare, and a very few female plants were found.

The Vivonne Bay material is dioecious, as was that studied by Boergesen (1931) from India, and Silva and Cleary (1954) from South Africa. Weber van Bosse (1896) stated that her only sexual plant was monoecious.

The genus *Platysiphonia*, based on *Sarcomenia miniata* (C. Agardh) J. Agardh, was described by Boergesen in 1931. He also suggested that *S. intermedia* and *S. mutabilis* should be placed in *Platysiphonia*. Boergesen based his new genus primarily on the great difference in size between *P. miniata* and the type species of *Sarcomenia* (*S. delesserioides*), and on the difference in thallus construction between them. The fact that a basal prostrate system is developed in *S. miniata* was also taken into consideration. At present the genus *Platysiphonia* includes *P. miniata* (C. Agardh) Boergesen, *P. mutabilis* (J. Agardh) Boergesen, *P. clevelandii* (Farlow) Papenfuss, *P. intermedia* (Grunow) Boergesen, and *P. parva* Silva & Cleary. *P. mutabilis* is described above as *Sarcomenia mutabilis*, though as shown later it is a species of *Platysiphonia*. *P. miniata* has been studied by Weber van Bosse (1896), Boergesen (1931), and Silva and Cleary (1954). A brief account only, based on the Vivonne Bay material, is given here.

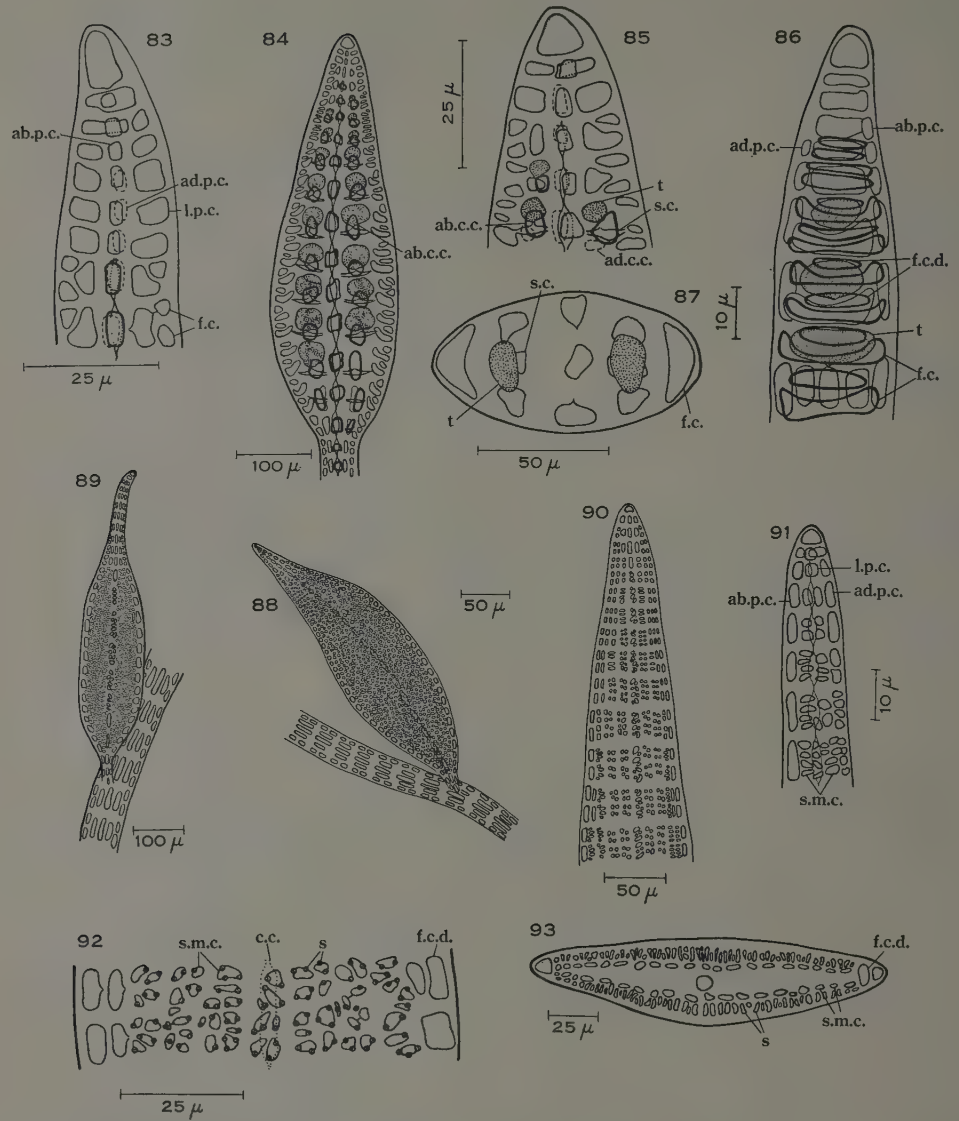
Structure of the thallus

In general structure and arrangement of cells *P. miniata* is essentially similar to *Sarcomenia victoriae* and *S. corymbosa*.

Growth is initiated by a hemispherical apical cell (Fig. 83). The abaxial pericentral cell is formed first, followed by the 2 lateral pericentral cells, and the adaxial pericentral cell is produced last. Weber van Bosse (1896) considered that the 2 lateral pericentral cells are formed first. Silva and Cleary (1954), however, found that the abaxial pericentral cell is formed first in South African material of *P. miniata*, and this is certainly so in the Vivonne Bay specimens. Two flanking cells are cut off by each lateral pericentral cell, and each elongates to half the length of the lateral pericentral cell. Lateral branches arise endogenously from the central cells, and pericentral cell formation follows as in the parent branch. The erect branches in *P. miniata* arise from prostrate basal branches which are attached to the substratum by unicellular rhizoids developed from the anterior flanking cells, usually on one side only. The thallus is ecorticate.

Development of stichidia and tetrasporangia

Stichidia develop as small lateral branches as in previously described species of the group, but very little if any cortication occurs even after the tetraspores are shed (Fig. 84). Each lateral pericentral cuts off first the tetrasporangium, followed by the abaxial cover cell, and last the adaxial cover cell (Figs. 85–87). The latter is about half the length of the transverse pericentral cells, and as the tetrasporangia


83
ab.p.c.
ad.p.c.
l.p.c.
f.c.
25 µ
84
ab.c.c.
100 µ
85
25 µ
t
s.c.
ab.c.c.
ad.c.c.
86
ab.p.c.
ad.p.c.
f.c.d.
t
f.c.
87
s.c.
t
f.c.
10 µ
50 µ
89
100 µ
88
50 µ
90
50 µ
91
l.p.c.
ab.p.c.
ad.p.c.
10 µ
s.m.c.
92
s.m.c.
c.c.
s
f.c.d.
25 µ
93
f.c.d.
25 µ
s.m.c.
s

Figs. 83–93.—*Platysiphonia miniata*. Fig. 83.—Branch apex, showing segmentation. Fig. 84.—A stichidium. Fig. 85.—Apex of a stichidium, showing formation of tetrasporangia and cover cells. Fig. 86.—The same, side view. Fig. 87.—Transverse section of a stichidium. Fig. 88.—Mature spermatangial blade in which the transverse pericentral cells have formed spermatangia. Fig. 89.—Spermatangial blade, showing partial division of transverse pericentral cells. Fig. 90.—Apex of a spermatangial blade, showing segmentation. Fig. 91.—Optical longitudinal view of apex of a young spermatangial blade, showing the transverse pericentrals (outer rows) and direct division of the lateral pericentral to form spermatangial mother cells without a residual cell. Fig. 92.—Surface detail of a spermatangial blade. Fig. 93.—Transverse section of a mature spermatangial blade.

mature all the cells of the stichidium separate further, so that at maturity the tetrasporangia receive little protection from either of the cover cells.

Weber van Bosse (1896) refers only to a dorsal (abaxial) cover cell formed before the tetrasporangium, but Silva and Cleary (1954) have also found that this was not so in South African material. Each flanking cell divides horizontally soon after its formation, cutting off a derivative anteriorly. These marginal cells elongate considerably and become strongly curved, especially the posterior one of each pair (Figs. 84, 86). In mature segments the marginal cells give as much, if not more, protection to the tetrasporangia as do the cover cells. No stichidia were seen with the posterior of each pair of marginal cells divided vertically as stated by Weber van Bosse (1896). Silva and Cleary (1954) found that the posterior cell usually remains undivided in South African material.

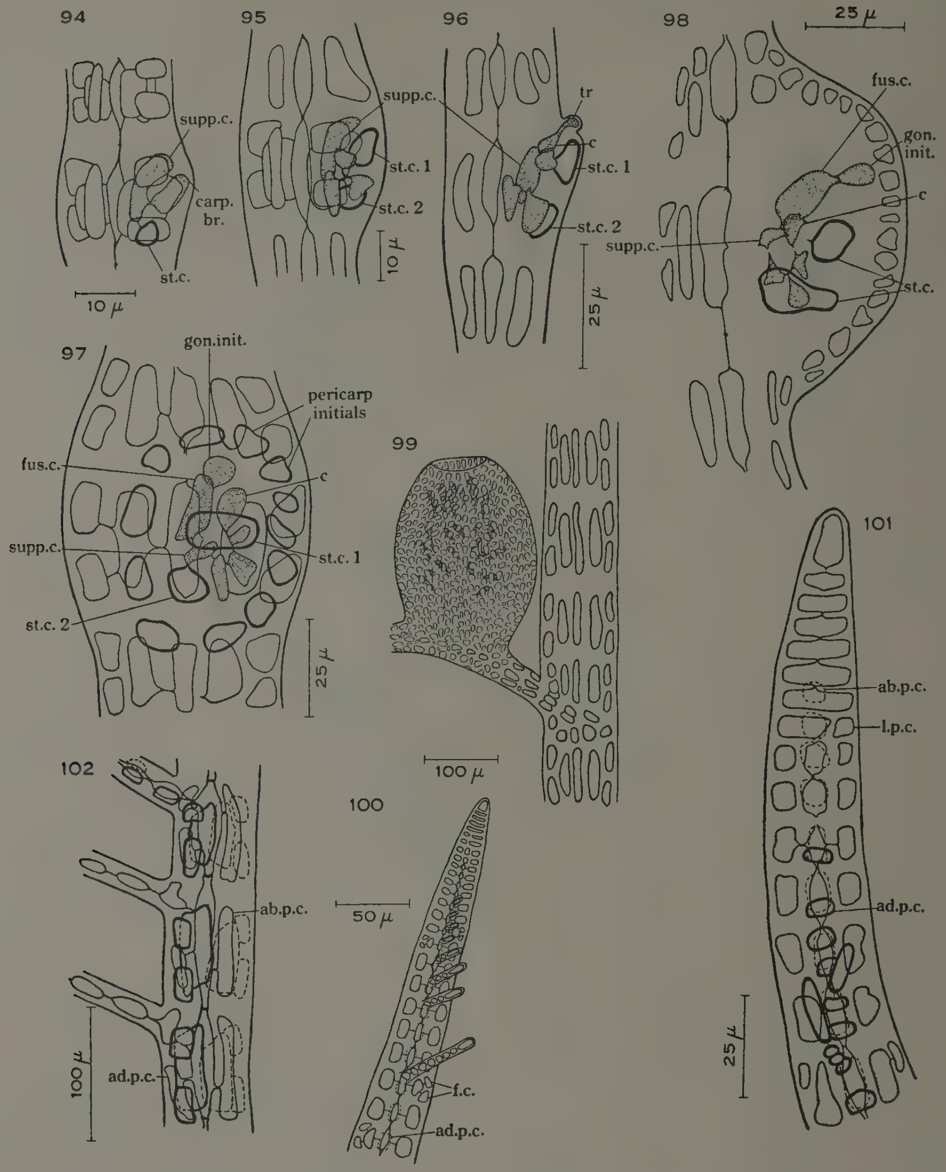
Development of spermatangial blades

The spermatia are formed on small lateral branches, similar to but more delicate than those previously described (Figs. 88, 89). They differ, however, in that the transverse pericentral cells are usually involved in spermatia production, and thus the branch lacks the distinct "midrib" of undivided pericentral cells (Fig. 88).

Boergesen (1931) also noted the activity of the transverse pericentral cells in spermatia production, but Weber van Bosse (1896) and Silva and Cleary (1954) found spermatia produced only from the lateral pericentral cells in South African material. Whether or not the transverse pericentral cells divide to form spermatia is apparently variable, since various stages showing partial involvement of the cells, or in some cases no divisions, were observed in the Vivonne Bay material. Figure 89 illustrates a spermatangial branch showing various degrees of division of the transverse pericentral cells. The flanking cells of the spermatangial branch of *P. miniata* divide longitudinally up to 3 times, and the first- and often the second-formed derivatives contribute to spermatia formation. On the margin of the blade a rather irregular line of undivided flanking cell derivatives remains, sometimes 1 and sometimes 2 cells wide (Fig. 90).

The lateral pericentral cells divide by a longitudinal periclinal wall into two, each of which divides anticlinally to give a row of 4 cells on each surface (Figs. 90, 91). Further anticlinal divisions may take place, giving on each surface 2 rows of up to 8 cells each from each lateral pericentral cell. These are the spermatangial mother cells. The derivatives of the flanking cells divide similarly but usually give a single row of 4 spermatangial mother cells. The transverse pericentral cells divide directly into a row of 4 spermatangial mother cells (Figs. 90, 91). Each spermatangial mother cell cuts off by oblique anticlinal walls 2–4 spermatangia (Figs. 92, 93).

Thus, in our spermatangial material of *P. miniata* there is no residual cell resulting from the first division of the lateral pericentral cells (Figs. 91, 93), in contrast to all other species of the *Sarcomenia* group. Boergesen (1931) found no residual cells in Indian material of *P. miniata*, but Silva and Cleary (1954) believed


94
supp.c.
carp. br.
st.c.
10 μ
95
supp.c.
st.c. 1
st.c. 2
10 μ
96
tr
c
st.c. 1
st.c. 2
25 μ
98
25 μ
fus.c.
gon. init.
c
supp.c.
st.c.
97
gon.init.
pericarp initials
fus.c.
c
supp.c.
st.c. 1
st.c. 2
25 μ
99
100 μ
101
ab.p.c.
l.p.c.
ad.p.c.
25 μ
102
ab.p.c.
ad.p.c.
100 μ
100
50 μ
f.c.
ad.p.c.

Figs. 94–99.—*Platysiphonia miniata.* Fig. 94.—A young procarp, with 1 sterile cell and the carpogonial branch initial. Fig. 95.—A young procarp, with a 3-celled carpogonial branch and 2 sterile cells. Fig. 96.—A mature carpogonial branch. Fig. 97.—Post-fertilization development of the fusion cell and initiation of the pericarp. Fig. 98.—Sectional view of a young cystocarp, showing development of the fusion cell. Fig. 99.—A mature cystocarp. Fig. 100.—*Cottoniella arcuata.* Branch apex, showing occasional formation of flanking cells and formation of endogenous monosiphonous filaments anterior to the adaxial pericentral cell (the latter shown by a broken line). Figs. 101, 102.—*Cottoniella filamentosa.* Fig. 101.—Branch apex, showing segmentation and formation of monosiphonous filaments anterior to the small adaxial pericentral cell. Fig. 102.—Side view of older part of a branch, showing origin of monosiphonous filaments.

him to be mistaken on the grounds that "in all Delesseriaceae the spermatangium mother cells represent cortical cells, at least in part".

Development of procarp

Both Weber van Bosse (1896) and Boergesen (1931) had only very limited female material of *P. miniata*, and only a very few of the Vivonne Bay plants were female. Weber van Bosse and Boergesen both described and figured the mature cystocarp, and Boergesen also described what he thought were stages in procarp development. He shows, however, a well-developed pericarp in his figures, and it seems likely, as Silva and Cleary (1954) have stated, that Boergesen was dealing with post-fertilization stages. In the Vivonne Bay material the pericarp is not initiated until after fertilization, as in all other species of the *Sarcomenia* group.

Procarps arise on the adaxial surface of young lateral branches which develop rapidly, so that the procarp and later the mature cystocarp occur near the base of a long branch. The adaxial pericentral cell cuts off 2 sterile cells and the initial cell of the carpogonial branch (Figs. 94, 95), the latter being formed before the second sterile cell. The carpogonial branch is 4-celled, the first cell becoming elongate and only lightly staining; the second cell is the largest (Fig. 96). The carpogonium bears a short trichogyne with a bulbous end, as in other members of the *Sarcomenia* group.

Development of cystocarp

Adequate material was not available to follow the post-fertilization development, but initial development of the fusion cell resembles that in previously described species (Figs. 97, 98). The pericarp is initiated after fertilization (Fig. 97). The mature cystocarp is relatively small (about 200 μ across), globose, and sessile on a short lateral branch (Fig. 99). The carposporophyte bears terminal carpospores but does not show the massive, erect basal part found in the species of *Sarcomenia* described above.

The pericarp is 2 cells thick. The inner erect filaments of cells each cut off 2 cells (sometimes 3 near the base) externally, but these cells remain more or less isodiametric in surface view and do not elongate horizontally. The very few cystocarps in the Vivonne Bay material agree with Boergesen's figure (1931, Fig. 5) but not with that of Weber van Bosse (1896, Fig. 9), who shows horizontally elongate cells.

2. **Cottoniella** Boergesen

Cottoniella was established by Boergesen (1919, p. 333) for an alga, from St. Thomas in the West Indies, which he named *C. arcuata*. A second species was added to the genus in 1920 when Boergesen transferred *Sarcomenia filamentosa* Howe (1905) which was based on a specimen from Cape Florida. *C. sanguinea* was described by Howe (1928) from Brazil and *C. fusiformis* by Boergesen (1930, p. 144) from the Canary Is. Schotter (1951), however, regarded *C. arcuata*, *C. filamentosa*, and *C. fusiformis* as forms of one species, in which he described a new variety *algeriensis* from Algeria.

A comparison of the published figures of *C. arcuata*, *C. fusiformis*, and Schotter's var. *algeriensis* shows certain marked differences. Boergesen's (1919, pp. 336, 337) figures of *C. arcuata* in general do not show flanking cells, yet when describing *C. fusiformis* Boergesen (1930) compares it with *C. arcuata* and *C. filamentosa* and states that all three species are closely related and almost identical in cell development. Flanking cells are formed regularly by each segment of *C. fusiformis* and *C. filamentosa*. *C. arcuata* var. *algeriensis* appears to be identical with *C. filamentosa*. The latter is discussed below on the basis of material from Florida. *C. fusiformis* is distinguished from the other taxa of *Cottoniella* by the formation of monosiphonous filaments, usually in pairs anterior to the adaxial pericentral cells. Boergesen states that this is not always so, but on present knowledge this appears to be an adequate character on which to separate *C. fusiformis* from the other species of *Cottoniella*.

In view of the discrepancy between Boergesen's original figures of *C. arcuata* (without flanking cells) and his later inferences of close resemblance between this species and others, type material from St. Thomas of *C. arcuata* has been examined. This material, kindly made available by Dr. Tyge Christenson, had been preserved in liquid in the Botanical Museum in Copenhagen, but had dried up. A small fragment was found amongst other algal material, as recorded by Boergesen. This material shows that Boergesen's figures are essentially accurate, but what he referred to as corticating cells (Boergesen 1919, Fig. 336*c* and probably 335*g*) are actually flanking cells which are formed only spasmodically along the branches. This is shown in our Figure 100. This appears to give a clear-cut distinction between *C. arcuata* and *C. filamentosa*, which otherwise are very similar.

On present knowledge it appears that *C. arcuata* Boergesen, *C. filamentosa* (Howe) Boergesen, and probably *C. fusiformis* Boergesen should be recognized as distinct species. Schotter's Algerian variety should be known as *C. filamentosa* var. *algeriensis* (Schotter) comb. nov. *C. sanguinea* Howe is discussed below.

Although *C. arcuata* only forms flanking cells occasionally, and the other species do so in each segment, the characteristic endogenous monosiphonous filaments formed anterior to the adaxial pericentral cells, and the characteristic habit of the species, indicate that they should be classed in one genus.

Reproductive organs are completely unknown in *Cottoniella*, but thallus structure allies it with other genera of the *Sarcomenia* group.

Cottoniella filamentosa (Howe) Boergesen 1920: 477.

Sarcomenia filamentosa Howe 1905: 571, pl. 29, fig. 6. De Toni 1924: 362. Schotter 1951: 279.

Type locality.—Florida (*Howe*).

Type.—In Herb. New York Botanical Garden (No. 2844).

The basic structure of *C. filamentosa* as given by Howe (1905), Boergesen (1919), and Schotter (1951), and as observed in material of *C. filamentosa* from Bald Point, Florida (coll. *H. J. Humm*), is summarized below.

Structure of thallus

The hemispherical apical initial cuts off segments which divide to form 4 pericentral cells. The abaxial pericentral cell is first formed, followed by the 2 lateral pericentral cells, and finally the adaxial pericentral cell (Fig. 101). Schotter (1951) states that the lateral pericentral cells are formed first in his Algerian material but Silva and Cleary (1954) found the abaxial pericentral to be formed first in *C. arcuata* from Bermuda. This is also true in the type material of *C. arcuata* Boergesen. The lateral pericentral cells each form 2 flanking cells each about half as long as the pericentral cell. This basic structure is typically that of the *Sarcomenia* group.

The distinctive feature of *Cottoniella* is the formation of monosiphonous filaments from the adaxial face of the branches. Cells of the filaments contain chromatophores. The filaments are conspicuous near the branch apices but fall off away from the tip. They develop endogenously from the central cell, at the anterior end of the adaxial pericentral cell, which is shorter in length than the other pericentral cells (Figs. 101, 102). They arise very shortly after the adaxial pericentral cell is formed. These filaments tend to emerge from the branch in 2 rows, alternately to either side. When the filaments are shed the basal cell only is retained. Monosiphonous filaments are not formed near the base of lateral branches; here the adaxial pericentral cell is about as long as the other pericentral cells.

The endogenous origin, anterior to the adaxial pericentral cell, of the monosiphonous filaments distinguishes *Cottoniella* from *Sarcomenia tenera* and *S. dolichocystidea*, where the filaments arise exogenously from the flanking cells or from the transverse pericentral cells. *Cottoniella hawaiiensis* Doty & Wainwright from the Hawaiian Is. lacks flanking cells except in the stichidia, and the monosiphonous filaments, superficially like those in *C. filamentosa*, arise exogenously from a lateral pericentral cell. These features separate *C. hawaiiensis* generically from *C. filamentosa* (see below).

Lateral branches arise endogenously from the central cells in *C. filamentosa* and cortication commences some distance from the apex and develops extensively, at least in some varieties. The thallus is attached by means of several-celled rhizoids from prostrate branches.

Cottoniella sanguinea Howe 1928

Cottoniella sanguinea Howe from Brazil is apparently known only from the type material. It is described as differing in the presence of 5 pericentral cells instead of 4.

The type material (NYBG, fragment in AD) is strongly adherent to the mounting paper and difficult to examine. Near the tip there appear to be only 4 pericentral cells, but 5 in older parts. In a few cases it appeared that the fifth cell might be cut off from one of the first 4 pericentrals but lie in the same circle of pericentral cells. The monosiphonous filaments were short and rather unlike those of *C. filamentosa*; their origin could not be determined. Flanking cells are not present.

C. sanguinea is probably not a species of *Cottoniella* though it may well belong to the *Sarcomenia* group, but its affinities cannot be established without better material.

3. **Cottoniella hawaiiensis** Doty & Wainwright 1958

Figs. 103–105

Doty and Wainwright (1958) have recently described a new species of *Cottoniella* from Hawaii. Their account, and an examination of type material kindly made available by Dr. M. S. Doty, shows, however, that this species cannot be placed in *Cottoniella*. A brief description and reasons for placing this alga in a new genus are given below.

The thallus consists of prostrate filaments attached to other algae by rhizoids and bearing lax unilateral branch systems up to 2 cm tall. The thallus is ecorticate, with 4 pericentral cells but no flanking cells in the vegetative parts (Fig. 103). The pericentral cells are formed in typical Rhodomelaceae fashion—abaxial, lateral, and adaxial in that order. Lateral branches arise endogenously from the adaxial surface of the thallus.

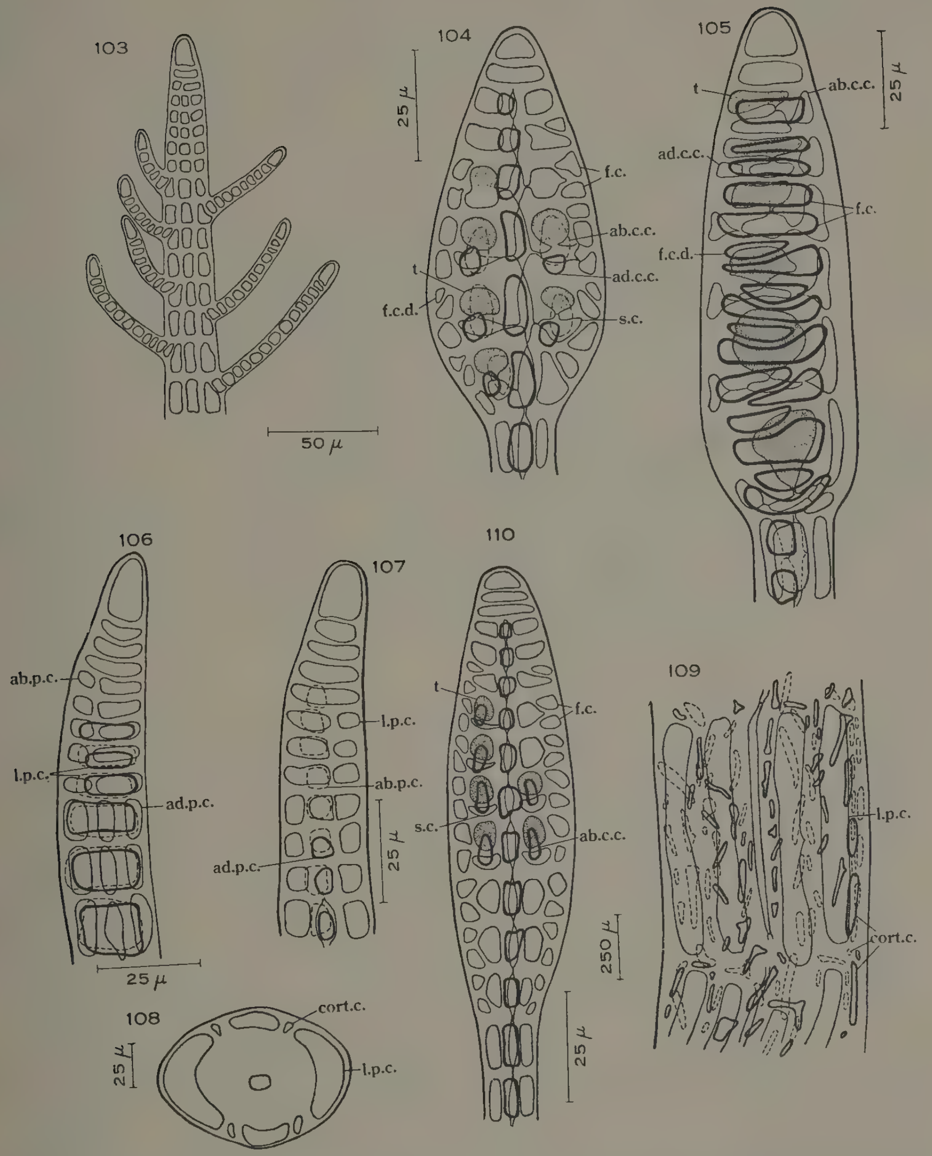
Monosiphonous filaments, containing chromatophores, are formed in characteristic manner from the lateral pericentral cells and are thus exogenous in origin. They occur alternately on the right and left pericentral cells of successive segments (Fig. 103), but are lost from older parts of the thallus. Branches tend to be concave towards the parent axis, and both rows of monosiphonous filaments are turned towards the concave side, i.e. adaxially.

The only reproductive organs known are stichidia. These are typical of the *Sarcomenia* group. The lateral pericentral cells each cut off 2 flanking cells (referred to by Doty and Wainwright as "cover" cells) which may each cut off a smaller cell (Figs. 104, 105). The tetrasporangium is cut off before the 2 cover cells on the abaxial and adaxial surfaces, of which the first-formed cover cell is extended anteriorly to partly protect the tetrasporangium while the last-formed cover cell is small and leaves the tetrasporangium exposed on that surface of the stichidium (Fig. 105). The flanking cells become curved and greatly extended horizontally, often with enlarged ends which give some protection to the tetrasporangia (Fig. 105). The flanking cell derivatives elongate but not to the same extent. Doty and Wainwright state that only an adaxial cover cell is formed, but both abaxial and adaxial cover cells are clearly present in our material. Doty and Wainwright also do not mention division of the flanking cells.

The stichidium, development and number of pericentral cells, and endogenous lateral branching clearly ally this plant with the *Sarcomenia* group. It differs from *Cottoniella*, however, in two important points:

(1) Flanking cells are completely lacking from the vegetative thallus.

(2) The monosiphonous filaments, superficially somewhat like those of *Cottoniella*, are exogenous in origin, from the lateral pericentral cells, whereas in *Cottoniella* they are endogenous, from the central cells.


103
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f.c.d.
105
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ab.c.c.
25 μ
ad.c.c.
f.c.
f.c.d.
106
ab.p.c.
l.p.c.
ad.p.c.
25 μ
107
l.p.c.
ab.p.c.
ad.p.c.
25 μ
110
t
f.c.
s.c.
ab.c.c.
250 μ
25 μ
109
l.p.c.
cort.c.
108
cort.c.
l.p.c.
25 μ

Figs. 103–105.—*Cottoniella hawaiiensis*. Fig. 103.—Branch apex, showing formation of exogenous monosiphonous filaments from the lateral pericentral cells. Fig. 104.—A young stichidium. Fig. 105.—Side view of a young stichidium, showing cover cells and flanking cells. Figs. 106–110.—*Polysiphonia roeana*. Fig. 106.—Side view of a slightly flattened branch apex, showing cell segmentation. Fig. 107.—Face view of a branch apex. Fig. 108.—Transverse section of a branch, with slight cortication. Fig. 109.—An older branch, showing cortication. Fig. 110.—A stichidium, showing tetrasporangia, cover cells, and flanking cells.

On these grounds *C. hawaiiensis* is considered generically distinct from *Cottoniella* and is renamed *Dotyella* in honour of Dr. Maxwell S. Doty (see below).

4. **Polysiphonia roeana** Harvey 1854: 540; 1858: pl. 35. J. Agardh 1863: 967; Kuetzing 1864: 20, t. 55*a–c*. De Toni 1903: 877.

Figs. 106–110; Plate 5, Fig. 1

Type locality.—Fremantle, W.A. (*Harvey*).

Type.—In Herb. Harvey (TCD), No. 169A.

Distribution.—Fremantle, W.A., Torrens Strait and American River Inlet on Kangaroo I., S.A. Sublittoral under calm conditions.

The thallus is composed of fine, much-branched filaments reaching a height of 20 cm (Plate 5, Fig. 1). The branches of the thallus frequently show a distinct, though slight, lateral flattening (Fig. 108). The thallus has a greyish iridescence when fresh which very quickly changes to rosy red on exposure or on confinement in a limited volume of water. Degeneration and decomposition of the thallus occur rapidly. The material studied was collected as drift at American River Inlet, Kangaroo I., in July 1947 (AD: A5784), August 1954 (AD: A19787), and May 1955 (AD: A21393). No fertile material was included in these collections, although some hundreds of plants of the August 1954 collection were examined. The material from Fremantle, originally described and figured by Harvey, was not fertile, and no reproductive organs have ever been described. However, a specimen in Adelaide University Herbarium (AD: A1459) from "Torrens Strait" (probably Torrens I. near Outer Harbour, S.A.) proved to be tetrasporic.

Structure of thallus

Growth is initiated by a large hemispherical apical cell, which cuts off disc-shaped segments posteriorly. These segments each form 4 pericentral cells around the central cell. The abaxial pericentral cell is the first formed (Figs. 106, 107), followed by the 2 lateral pericentral cells, and finally by the adaxial pericentral cell. In the vegetative parts no lateral flanking cells are produced after the formation of the 4 pericentral cells. The cells of each segment elongate considerably, until in the older corticated branches each segment measures up to 1 mm in length. Small, elongate corticating cells are formed in fairly regular longitudinal rows from the external surfaces of each pericentral cell (Fig. 109). Lateral branches are endogenous in origin, developing from the anterior end of the central cell of the parent branch. Branching is largely from the adaxial face of the parent branch. The branches show a definite, although slight, lateral flattening, due to the larger diameter of the lateral pericentral cells (Fig. 108). The typical trichoblasts of *Polysiphonia* are completely absent.

Development of stichidia and tetrasporangia

The single dried tetrasporic specimen of *P. roeana* available did not prove suitable for a detailed study of stichidial development, but the broad features can be given with some assurance.

Tetrasporangia form near the ends of lateral branches and the stichidia are less well defined than in other species of the *Sarcomenia* group. Small lateral branches may be largely fertile, but more usually only the end 10 or more segments of a long lateral branch bear tetraspores. The order of cell formation in the stichidium could not be followed, but it is clear (Fig. 110) that:

(1) Typical flanking cells are produced by all fertile segments of the flattened stichidium, but they appear to remain undivided.
(2) Tetrasporangia are produced in 2 longitudinal rows from the lateral pericentral cells.
(3) Adaxial and abaxial cover cells appear to be formed.
(4) The tetrasporangia are only partly protected by the cover cells and the flanking cells. The latter become elongate and curved, but not to the same extent as in previously discussed species of the *Sarcomenia* group.
(5) The tetraspores are tetrahedrally divided.

The affinity of Polysiphonia roeana

The order of pericentral cell formation, absence of trichoblasts, tendency to slight flattening of the thallus, rapid disintegration of the thallus under drying or crowding after collection, and the typical *Sarcomenia*-type stichidia all point to *P. roeana* being a member of the *Sarcomenia* group. The absence of flanking cells in the vegetative thallus separate it from all other genera of the group except *Dotyella hawaiiensis*. The relationships of *P. roeana* are further discussed below.

5. **Taenioma** J. Agardh

Taenioma is usually referred to the *Sarcomenia* group. It has been investigated in detail by Papenfuss (1944) and Tseng (1944), who had only tetrasporic material. The only record, with brief descriptions, of cystocarpic and spermatangial material is that of Thompson (1910), on *T. perpusillum*, though Dickinson and Foote (1950) reported female material from the Gold Coast. Desikachary and Balakrishnan (1957) described vegetative and tetrasporic *T. perpusillum* and vegetative *T. nanum* from India. Tetrasporic *T. perpusillum* is known from South Australia (Scott's Bay on Eyre Peninsula, and Second Valley, both specimens in AD), and agrees well with the descriptions of Papenfuss and Tseng. *T. perpusillum* has been recorded from Queensland by Cribb (1954, p. 26).

Taenioma is a most distinctive genus, particularly in the presence of indeterminate and determinate branches, the latter surmounted by 2 or 3 long hairs. Flanking cells occur only on the determinate branches.

Taenioma differs from other genera of the *Sarcomenia* group in that the order of pericentral cell formation is typically delesseriaceous, i.e. the 2 lateral pericentrals are formed first. The apical hairs, which may be interpreted as monosiphonous filaments formed only on the distal 2 or 3 segments, complicate the position, however, and perhaps undue weight should not be placed on this difference in pericentral cell formation. Although the hairs appear to be meristematic near their bases, Papenfuss has shown this to be due to more rapid elongation of the upper cells after cell division of the terminal cell ceases. The upper parts at least of the hairs are also colourless, in contrast to the assimilatory nature and longer-retained apical meristem of the monosiphonous filaments of *Cottoniella*, *Sarcotrichia*, and *Dotyella*.

Lateral branches in *Taenioma* arise exogenously, in contrast to other genera of the *Sarcomenia* group.

The formation of flanking cells, tetrasporangia, and cover cells is similar to that in other members of the *Sarcomenia* group. The flanking cells, however, do not divide and do not elongate horizontally and curve so as to partially protect the tetrasporangia as in other species. The tetrasporangia in *Taenioma* are virtually unprotected on either face of the stichidium.

Thompson (1910) describes spermatangial branches and also the mature cystocarp of *T. perpusillum*. Spermatangia are formed on the determinate branches, ultimately covering the whole surface. The flanking cells first divide, and the inner derivatives as well as the lateral pericentral cells are involved in spermatia formation. The transverse pericentrals and outer flanking or marginal cells remain as distinct lines of larger undivided cells. Thompson does not mention residual cells from the first divisions of the lateral pericentral cells, and this point is doubted by Papenfuss (1944, p. 203) since residual cells are normally present in Delesseriaceae. Papenfuss (personal communication) has since examined cystocarpic and spermatangial material of *T. perpusillum* from the Gold Coast and states that residual cells are present in the spermatangial blades.

Thompson (1910) also describes the structure of mature cystocarps. These are borne on terete branches and are urceolate in shape with a prominent neck and osteole. The wall consists of an outer layer of angular cells with inner filaments of cells running from the base to the osteole. The gonimoblast shows a large, erect, basal cell from which branched filaments of cells arise with terminal carpospores. This cystocarp appears to be very similar in structure to that of *Platysiphonia miniata* and others of the *Sarcomenia* group.

V. The Distinctive Features of the Sarcomenia Group

The genera and species which have been described above are usually classed together as the *Sarcomenia* group and placed in the Delesseriaceae. They have the following features in common.

(1) Thallus with 4 pericentral cells, the 2 lateral pericentral cells larger than the transverse ones, and each producing (at least in the stichidia) 2 flanking cells each about half the length of the pericentral cells.

(2) The abaxial pericentral cell is first formed, followed by the 2 lateral pericentral cells, and finally the adaxial pericentral cell. (Exception: *Taenioma.*)

(3) Each cell contains numerous ovoid to elongate chromatophores.

(4) The complete absence of typical rhodomelaceous trichoblasts, but the presence in certain genera (*Sarcotrichia*, *Cottoniella*, *Dotyella*, and *Taenioma*) of monosiphonous chromatophore containing filaments which arise exogenously (Exception: *Cottoniella.*) from the pericentral cells.

(5) Lateral branches develop endogenously. (Exception: *Taenioma.*)

(6) Stichidia with 2 longitudinal rows of tetrahedrally divided sporangia formed from the lateral pericentral cells prior to the formation of both adaxial and abaxial cover cells. The abaxial cover cell is usually larger than the adaxial and gives

some protection to the tetrasporangium, whereas the latter is largely exposed on the adaxial side. The flanking cells extend horizontally, frequently curve, and give some protection to the tetrasporangium. Division of each flanking cell horizontally into two occurs in most species.

(7) Spermatangial blades show division of the lateral pericentrals into cortical cells on each surface, leaving a central residual cell. (Exceptions: *Platysiphonia miniata*, *Taenioma perpusillum?*)

The cortical cells divide anticlinally to form spermatangial mother cells, each of which forms 2–4 spermatangia. Derivatives of the flanking cells may also form spermatangia, with (e.g. *S. delesserioides*) or without (*P. miniata*, *P. parva*) the formation of residual cells.

The spermatangial blade usually shows a margin of one or more rows of undivided cells (flanking cells or their derivatives) and a central row of undivided transverse pericentral cells. (Partial exception: *P. miniata*.)

(8) Procarps arise on the adaxial side only of young branches, from the adaxial pericentral cell which acts as the supporting cell. A first sterile cell, the carpogonial branch initial, a second sterile cell, and then the other 3 cells of the carpogonial branch develop in that order. The second cell of the carpogonial branch is usually the largest and is often binucleate. The carpogonium bears a short trichogyne with a bulbous end. Normally only 1 procarp per branch develops.

Following fertilization, the anterior end of the supporting cell is cut off as the auxiliary cell, and fusion occurs between this and the carpogonium by means of a short tube. Other cells may or may not fuse, and the fusion cell becomes more or less erect and often elongate, developing gonimoblast filaments sympodially with terminal carposporangia.

The 2 sterile cells eventually disintegrate as the gonimoblast develops. If fertilization does not occur they may, in some species, divide further and contribute to cortication of the blade. The pericarp is initiated from the pericentral and flanking cells after fertilization, and develops an urceolate shape with a terminal osteole. The wall consists of inner erect filaments not connected laterally, which cut off externally 2 (rarely 3) cells each. These outer cells may be arranged horizontally or vertically; if the latter they usually elongate horizontally and separate considerably in the mature cystocarp.

(9) The thallus when living is usually an iridescent greyish red, but on exposure to air or crowding after collection rapidly turns rosy red and disintegrates. (*Dotyella* and *Taenioma* are unknown in this respect.)

VI. The Genera and Species of the Sarcomenia Group

Various authors, including Grunow (1870), J. Agardh (1899), Howe (1905), and Boergesen (1920) have realized that *Sarcomenia* was not a natural genus, but owing to the difficulties of studying dried material little could be done to clarify the group. Boergesen (1919) described *Cottoniella* and later (1931) segregated *Platysiphonia*.

The most important changes now made are the inclusion of several other species in *Platysiphonia*, and the two species with monosiphonous filaments (*S. tenera*, *S. dolichocystidea*) in a new genus, *Sarcotrichia*. *Platysiphonia* now includes eight species which differ most conspicuously in size and degree of cortication but are similar in fundamental structure. Only one species, *S. delesserioides* Sonder, is now left in *Sarcomenia*. *Polysiphonia roeana* Harvey has been shown above to be almost certainly a member of this group, and is here placed in a new genus, *Malaconema*.

Generic differences within the group are based largely on vegetative structure since reproductive organs, where known, are very similar. A key to the genera is given below, followed by brief taxonomic diagnoses.

KEY TO GENERA OF THE SARCOMENIA GROUP

1. Thallus without flanking cells from the lateral pericentral cells of vegetative (indeterminate) branches 2
1. Thallus with flanking cells from the lateral pericentral cells 4
    2. Thallus without monosiphonous filaments .... *Malaconema*
    2. Thallus with monosiphonous filaments 3
3. Monosiphonous filaments from the lateral pericentral cells, turned to the adaxial side .... *Dotyella*
3. Monosiphonous filaments in 2's or 3's surmounting determinate branches .... *Taenioma*
    4. Free monosiphonous filaments present 5
    4. Free monosiphonous filaments not formed 6
5. Monosiphonous filaments formed endogenously from the central cells anterior to the adaxial transverse pericentral cell .... *Cottoniella*
5. Monosiphonous filaments formed exogenously from the anterior flanking cells of each segment and in *S. tenera* from the transverse pericentrals .... *Sarcotrichia*
    6. Flanking cells not dividing further in the vegetative thallus .... *Platysiphonia*
    6. Flanking cells dividing further, the anterior one producing 2 chains of cells, the posterior one a single chain of cells, which remain laterally adherent giving a strongly compressed thallus .... *Sarcomenia*

Sarcomenia Sonder 1845. Type and only species: *S. delesserioides* Sonder 1845.

Thallus arising from a branched holdfast, erect, to 50 cm high; branches strongly flattened, up to 2 cm broad. Branching endogenous from the central cells, issuing usually to the side of the midrib. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells, the upper of which forms 2 chains of cells, the lower 1 chain of cells, all lying in the one plane and laterally adherent to form the broad, flat branches; cell divisions restricted to the marginal end cells of the chains. Thallus heavily corticated to near the apices.

Cystocarps and stichidia corticated. Spermatangia formed from lateral pericentral cells and several series of flanking cell derivatives. Otherwise reproductive organs as in the *Sarcomenia* group.

Platysiphonia Boergesen 1931. Type species: *P. miniata* (C. Agardh) Boergesen.

Thallus arising from a prostrate basal part attached by rhizoids or from a branched holdfast, variable in size. Branches compressed when young, becoming more or less terete when corticated. Lateral branches endogenous from the central cells, issuing above or laterally to the central cells. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells which do not divide further (except in the spermatangial branches of certain species). Thallus varying from ecorticate in some species to heavily corticate in others. Cystocarps and stichidia not or only slightly corticated near the base. Reproductive organs as in the *Sarcomenia* group.

Platysiphonia includes the following species as well as the type:

P. intermedia (Grunow) Boergesen 1931.
P. mutabilis (Harvey) Boergesen 1931.
P. clevelandii (Farlow) Papenfuss 1944.
P. parva Silva & Cleary 1954.
P. victoriae (Harvey ex J. Agardh) comb. nov. (*Sarcomenia victoriae* Harvey ex J. Agardh 1863: 1262.)
P. corymbosa (J. Agardh) comb. nov. (*Sarcomenia corymbosa* J. Agardh 1896: 134.)
P. hypneoides (Harvey) comb. nov. (*Sarcomenia hypneoides* Harvey 1854: 537.)

KEY TO THE SPECIES OF PLATYSIPHONIA

1. Thallus to a few centimetres high, not or only very slightly corticate 2
1. Thallus 6–40 cm high, heavily corticate below 5
  2. Flanking cells of stichidium undivided 3
  2. Flanking cells of stichidium divided into two 4
3. Thallus to 1 cm high, epiphytic on *Codium* (Guadalupe Is.) ......*P. parva* Silva & Cleary
3. Thallus not epiphytic on *Codium*, to 8 cm high (South Africa, St. Paul) ....*P. intermedia* (Grunow) Boergesen
  4. Flanking cells in stichidium divided horizontally into two. Lateral branches emerging in line with the longitudinal axis of the parent branch ....*P. miniata* (C. Agardh) Boergesen
  4. Flanking cells in stichidium divided vertically giving an outer marginal row of cells. Lateral branches emerging obliquely laterally from the longitudinal axis of the parent branch ....*P. clevelandii* (Farlow) Papenfuss
5. Branching mostly unilateral from the adaxial surface of parent branches ....*P. corymbosa* (J. Agardh) comb. nov.
5. Branching more irregular 6
  6. Branches corticate only near their bases, plant relatively slender ....*P. mutabilis* (Harvey) Boergesen
  6. Branches corticate nearer their apices, plant robust, stem to 2 mm thick below 7
7. Branches corticate almost to the apices, branch ends curled, stichidia corticate ....*P. hypneoides* (Harvey) comb. nov.
7. Younger branches and stichidia ecorticate ..*P. victoriae* (Harvey ex J. Agardh) comb. nov.

Sarcotrichia gen. nov. Type species: *S. tenera* (Harvey) comb. nov. (*Dasya tenera* Harvey 1854: 543.)

Thallus arising from a branched holdfast, to 30 cm high. Branches compressed above, more or less terete and heavily corticate below. Lateral branches endogenous from the central cells. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells. Anterior flanking cells (and in *S. tenera* the transverse pericentral cells also) forming slender, monosiphonous filaments from their anterior ends;

filaments completely free, deciduous on older branches. Cystocarps and stichidia not corticated. Spermatangia on small lateral blades.

Thallus oriens ex haptero ramoso, ad 30 cm altus. Superni rami compressi, inferne rami teretiores et corticatissimi. Laterales rami endogeni e cellulis centralibus. 4 cellulae pericentrales; quaque cellula latero-pericentralis producens 2 marginales cellulas. Cellulae marginales anteriores (et in *S. tenera* etiam cellulae pericentrales transversae) producentes tenuia, monosiphona filamenta ex anterioribus extremis; filamenta toto separata, cadentia in ramis maturis. Cystocarpia et stichidia non corticata. Spermatangia in ramulis lateralibus.

Sarcotrichia also includes *S. dolichocystidea* (J. Agardh) comb. nov. (*Sarcomenia dolichocystidea* J. Agardh 1896: 135.)

Key to the Species of Sarcotrichia

1. Monosiphonous filaments produced from the anterior flanking cells and the transverse pericentral cells .... *S. tenera* (Harvey) comb. nov.
1. Monosiphonous filaments produced from the anterior flanking cells only .... *S. dolichocystidea* (J. Agardh) comb. nov.

Cottoniella Boergesen 1919. Type species: *C. arcuata* Boergesen 1919.

Thallus slender, arising from prostrate parts attached by rhizoids, up to 12 cm high, corticate below. Lateral branches endogenous, above more or less arcuate. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells (only occasional in *C. arcuata*) which do not divide further. Monosiphonous filaments formed endogenously from the central cells, anterior to the adaxial pericentral cell, in 1 or 2 rows. Reproductive organs unknown.

Dotyella gen. nov. Type species: *D. hawaiiensis* (Doty & Wainwright) comb. nov. (*Cottoniella hawaiiensis* Doty & Wainwright 1958: 229.)

Thallus slender, to 2 cm high, with erect branches arising from prostrate parts attached by rhizoids; ecorticate. Lateral branches endogenous from the central cells. Pericentral cells 4. No flanking cells formed in vegetative parts. Monosiphonous filaments arising from the lateral pericentral cells, alternately on opposite sides, turned towards the adaxial side of the branch. Stichidia with flanking cells, developing as in the *Sarcomenia* group. Cystocarps and spermatia unknown.

Thallus tenuis, ad 2 cm altus, cum ramis erectis orientibus e partibus prostratis adfixis a rhizoidibus; ecorticatus. Laterales rami endogeni e cellulis centralibus. 4 cellulae pericentrales. Marginales cellulae deficientes in partibus sterilibus. Filamenta monosiphona orientia e cellulis latero-pericentralibus et alternato in lateribus oppositis, versa ad adaxiale latus rami. Stichidia marginalibus cellulis sicut in Sarcomenioideis. Cystocarpia et spermatia incognita.

Malaconema gen. nov. Type species: *M. roeana* (Harvey) comb. nov. (*Polysiphonia roeana* Harvey 1854: 540.)

Thallus very slender, to 20 cm high, terete or slightly flattened. Lateral branches irregular, endogenous from the central cells. Thallus lightly corticate below. Pericentral cells 4, the 2 lateral ones largest. No flanking cells formed in vegetative parts. No monosiphonous filaments formed. Ends of tetrasporangial branches broader, similar to stichidia of the *Sarcomenia* group. Stichidia with 2 flanking cells formed from each lateral pericentral cell. Cystocarps and spermatangial branches unknown.

Thallus tenuissimus, ad 20 cm altus, teres aut compressior. Rami laterales irregulares, endogeni e centralibus cellulis. Thallus paulum corticatus inferne. 4 cellulae pericentrales, quarum 2 laterales cellulae maximae. Marginales cellulae deficientes in partibus sterilibus. Filamenta monosiphona deficientia. Fines tetrasporangialium ramorum latiores sicut stichidia Sarcomeneoidearum. Stichidia cum 2 marginalibus cellulis formatis ex quaque cellula latero-pericentrali. Cystocarpia et spermatia incognita.

Taenioma J. Agardh. Type species: *T. perpusillum* (J. Agardh) J. Agardh. (*Polysiphonia perpusilla* J. Agardh.)

Thallus minute, with prostrate, terete, indeterminate branches attached by rhizoids and with 4 pericentral cells only, and erect, flattened, determinate branches arising from the indeterminate branches. Determinate branches with 2 flanking cells from each lateral pericentral, the whole branch surmounted by 2 or 3 long monosiphonous filaments. Tetrasporangia and spermatangia formed in determinate branches, cystocarps on terete branches.

VII. Taxonomic Relationships of the Sarcomenia Group

Sarcomenia, when originally described by Sonder (1845, p. 56; 1846, p. 194) was placed in the Delesserieae, and this was followed by Kuetzing (1849). At this time *S. delesserioides* Sonder was the only known species of the genus. Harvey (1847, 1854, 1860), however, suggested that it belonged to the Rhodomeleae, and this was supported by J. Agardh (1863) when he described several other species of *Sarcomenia*, based largely on Harvey's collections. J. Agardh described the tribe Sarcomenieae of the order Rhodomeleae, including in it *Taenioma*, *Vanvoorstia*, and *Claudea* as well as *Sarcomenia*. The distinctive feature of this tribe was the presence of half-length marginal cells outside the lateral pericentral cells. Later J. Agardh (1896, 1899) discussed the species of *Sarcomenia* remarkably thoroughly considering that he had only dried material, and he considered that the group definitely belonged to the Rhodomeleae. Schmitz (1889) and Schmitz and Hauptfleisch (1897), however, placed the Sarcomenieae as a subfamily of the Delesseriaceae, distinguished from the rest of the Delesseriaceae by the tetrasporangia being formed in a single layer only and by the prominent globose cystocarps. They included in the Sarcomenieae the following genera: *Caloglossa*, *Taenioma*, *Sarcomenia*, *Sonderella*, *Claudea*, *Vanvoorstia*, and *Zellera*.

Falkenberg (1901) strongly supported the affinities of the *Sarcomenia* group with the Delesseriaceae, and strongly criticized J. Agardh's placing of it as a tribe of the Rhodomelaceae. Falkenberg used two features in particular in placing the Sarcomenieae in the Delesseriaceae, viz. the method of division of the apical cell to form pericentral cells, and the cutting off by the lateral pericentral cells of two marginal or flanking cells each half the length of the pericentral cells. The order of pericentral cell formation, first elucidated by Naegeli (1847), is probably still the best character on which to separate the Rhodomelaceae and Delesseriaceae, but Falkenberg apparently based his concepts of the *Sarcomenia* group on *Taenioma*, whereas J. Agardh had studied in considerable detail the species of *Sarcomenia* itself. As is shown in the present study, all the species then placed in *Sarcomenia* show the rhodomelaceous order of pericentral cell formation, whereas *Taenioma* is exceptional (for the *Sarcomenia* group) in showing the delessereaceous order of pericentral cell formation.

More recent authors who have studied members of the *Sarcomenia* group have not had adequate material on which to form opinions on the position of the group. Papenfuss (1944) and Tseng (1944) both studied *Taenioma perpusillum*, and support Falkenberg's findings.

From the Sarcomenieae as recognized by Schmitz and Hauptfleisch, *Caloglossa*, *Claudea*, and *Vanvoorstia* have been separated by Papenfuss (1937) as the *Claudea* group; *Caloglossa*, however, was later removed from this group by Papenfuss (1944) because of its exogenous branching and is placed by Kylin (1956) in a group of its own. *Zellera* is little known but probably belongs also to the *Claudea* group. *Sonderella* is not a member of the group but belongs to the Rhodomelaceae, possibly near the *Amansia* group; this will be discussed in a separate account.

The *Sarcomenia* group thus contains *Sarcomenia*, *Platysiphonia*, *Cottoniella*, and *Taenioma*, and the three genera described in this account: *Sarcotrichia*, *Malaconema*, and *Dotyella*. The distinctive features of these genera have been outlined above, and can now be discussed further in relation to the taxonomic position of the *Sarcomenia* group.

Recent discussion of the *Sarcomenia* group has centred mainly on whether it should be recognized as an independent subfamily of the Delesseriaceae or merged with the Delesserieae. Kylin (1923, 1928) first advocated the latter course, on the grounds that the procarps were formed on the midrib of the blade, in contrast to the Nitophylleae, where they occur scattered over the surface. Kylin (1924 and previously), however, while studying in detail many Delesserieae and Nitophylleae, did not study any members of the Sarcomenieae. Kylin was supported by Papenfuss (1937) on the basis of a study of *Claudea* and *Vanvoorstia* and by Papenfuss (1944) on *Taenioma*, but the first two genera are not members of the *Sarcomenia* group and *Taenioma* is certainly not a typical representative. Fritsch (1945, p. 746), however, retains the Sarcomenieae as a distinct subfamily of the Delesseriaceae. The present study shows that there are other features more significant than the procarp position which separate the *Sarcomenia* group from the Delesseriaceae.

(*a*) *Vegetative Features*

The order of pericentral cell formation in all genera of the *Sarcomenia* group except *Taenioma* is the abaxial pericentral cell first, followed by the 2 lateral pericentral cells, and finally by the adaxial pericentral cell. This order is typical of the Rhodomelaceae, in contrast to the Delesseriaceae, where the lateral pericentral cells are first formed; and since being elucidated by Naegeli (1847) this has proven one of the most satisfactory distinctions between the two families. Papenfuss (1944, p. 200) states that not a single exception to this separation of the two families has been found. This, however, was before the *Sarcomenia* group had been adequately investigated and, as stated before, the example of this group (*Taenioma*) studied by Falkenberg, Papenfuss, and others is exceptional in its pericentral cell formation. The situation in *Taenioma* is not easy to evaluate owing to the restriction of monosiphonous filaments to the apex of the branches and the very rapid formation of determinate and indeterminate apices at the branch ends.

If the distinction on pericentral cell formation is regarded as of primary importance, then the *Sarcomenia* group must be classed under the Rhodomelaceae, and *Taenioma* must be regarded as doubtfully a member of the group.

A more important exception to the above separation of the families Delesseriaceae and Rhodomelaceae occurs in the *Claudea* group of the former, where *Claudea* shows the delesseriaceous plan but *Vanvoorstia* the rhodomelaceous plan of pericentral cell formation (see Section IX).

Other vegetative features of the *Sarcomenia* group indicate that its affinities are with the Delesseriaceae rather than the Rhodomelaceae, but exceptions are known in each case.

All Delesseriaceae possess 4 pericentral cells, whereas the basic number (at least in fertile parts) in the Rhodomelaceae is 5. In this respect the *Sarcomenia* group is similar to the Delesseriaceae.

In the Delesseriaceae the first-formed pericentral cells lie in a row, whereas in many Rhodomelaceae but not all they are spirally arranged. In the *Sarcomenia* group the first-formed pericentral cells lie in a linear row.

The Delesseriaceae without exception lack typical trichoblasts, which are a feature of most but not all of the Rhodomelaceae. Typical trichoblasts are strictly exogenous (Scagel 1953, p. 9) and arise very close to the apical cell before the ring of pericentral cells is fully developed. They are usually colourless, lacking chromatophores (exception: Lophothalieae), and almost always bear the sex organs. Trichoblasts are not known in *Bostrychia* or in the vegetative state of *Polyzonia* (Scagel 1953, p. 8). The monosiphonous filaments of certain genera of the *Sarcomenia* group (*Sarcotrichia*, *Dotyella*), are exogenous but do not arise till after pericentral cell formation, while those of *Cottoniella* are endogenous from the central cells. In these genera of the *Sarcomenia* group the cells of the monosiphonous filaments contain abundant chromatophores. They appear therefore to be distinct in both origin and structure from typical trichoblasts.

The presence of flanking cells, produced in pairs from the lateral pericentral cells, has been regarded as a distinctive character of the Delesserieae. This was one of the main reasons why Falkenberg (1901) and others referred the *Sarcomenia* group to the Delesseriaceae. In most Delesserieae the flanking cells give rise to initials which produce rows of cells. In a few genera of Rhodomelaceae where flanking cells are formed, only one is cut off by each pericentral cell and this later divides lengthwise into two (Papenfuss 1944, p. 201). The *Sarcomenia* group resembles the Delesserieae in that both flanking cells originate directly from the lateral pericentral cells. In certain genera, however, flanking cells are formed only in the stichidia.

Branching in the Rhodomelaceae is basically exogenous, originating close to the apical cell, but endogenous branches occur in *Metamorphe*, the Amansieae, and the Lophosiphonieae (Scagel 1953, p. 9; Kylin 1956). The Delesserieae show endogenous branching exclusively except for *Caloglossa* (and *Taenioma*) (Papenfuss 1944, p. 207). Branching in the *Sarcomenia* group is endogenous except for the monosiphonous filaments in *Sarcotrichia* and *Dotyella*.

While the form and habit of *Sarcomenia delesserioides* is delesseriaceous, that of other species of the *Sarcomenia* group is distinctly rhodomelaceous or dasyaceous, as the thalli in general are more or less terete and much branched.

Thus while the most important vegetative distinction between the Delesseriaceae and Rhodomelaceae, the order of pericentral cell formation, places the *Sarcomenia* group in the Rhodomelaceae (which it also resembles in general appearance), other vegetative features show similarity with the Delesseriaceae.

(*b*) *The Procarp and Cystocarp*

Papenfuss (1944, p. 203), following similar expressions by earlier authors, states that there are "no sharply defined and constant differences between the Rhodomelaceae and Delesseriaceae with respect to the development and structure of the cystocarp". Kylin (1956), however, separates these two families primarily on the method of branching of the gonimoblast filaments. This is monopodial in the Delesseriaceae and sympodial in the Rhodomelaceae. This distinction was first recognized by Falkenberg (1901) but has not been emphasized by other authors except Kylin. The use of this feature warrants further careful investigation, and some doubt may be felt as to its significance from figures given by Kylin (1956) of gonimoblasts in various Delesseriaceae and Rhodomelaceae.

The gonimoblast development in the *Sarcomenia* group is sympodial, if somewhat irregular, and Kylin would doubtless have placed it in the Rhodomelaceae had he known this.

The position of the procarp provides a good distinction between the Delesseriaceae and Rhodomelaceae, with a few exceptions in the latter family. In the Delesseriaceae the procarp is always borne directly on the blades, but in the Rhodomelaceae it occurs on trichoblasts with few exceptions (*Rhodomela*, *Bostrychia*). In this respect the *Sarcomenia* group agrees with the Delesseriaceae.

Procarps in the Delesserieae (excluding the *Claudea* group) are formed on both surfaces of the blade, but in the *Sarcomenia* group they occur on only one series (adaxial) of transverse pericentral cells. The 2 sterile cells of the procarp of the *Sarcomenia* group ultimately disintegrate unless fertilization does not occur, when they may divide in some species and contribute to cortication of the blade. In this respect they are similar to the sterile cells in the Delesserieae (Kylin 1923, p. 102; 1937, p. 286; Papenfuss 1944, p. 210).

Carpospores in the *Sarcomenia* group are produced singly and terminally, as they are also in the *Claudea* group. In other groups of the Delesserieae carpospores are produced in rows (Kylin 1956, p. 417). In the Nitophylleae and Rhodomelaceae carpospores are also formed terminally and singly.

The mature cystocarp of the *Sarcomenia* group is an external, urceolate structure similar to that in most Rhodomelaceae. The cystocarp of the Delesseriaceae in contrast is partly or largely immersed in the thallus. The pericarp is initiated after fertilization in most Delesseriaceae, whereas in most Rhodomelaceae (one exception is *Bostrychia* (Fritsch 1945, p. 707)) it is initiated before fertilization. In the *Sarcomenia* group the pericarp is not initiated until after fertilization.

The pericarp wall of the Delesseriaceae cystocarp usually consists of several layers of cells of similar size, arranged in vertical rows and originating from the cortical cells which surround the procarp (Kylin 1956, p. 415) or sometimes from the pericentral cells. In the Rhodomelaceae the pericarp is normally 2 cells thick, formed of an inner layer of erect filaments, the cells of which each cut off 2 or 3 outer cells (which may be interpreted as pericentral cells). Further cortication occurs in some species. The pericarp of the *Sarcomenia* group cystocarp is of the latter type, and the 2 (or 3) outer cells, cut off from each vertical filament cell, may lie horizontally or one above the other. In the latter case they become considerably elongate horizontally. The mature pericarp cells separate considerably from each other.

Thus while differences in procarp and cystocarp structure between the Delesseriaceae and Rhodomelaceae are mostly relatively minor, the position of the procarp of the *Sarcomenia* group is more typically delesseriaceous, but Kylin's distinction of the families on the method of gonimoblast branching would definitely place the *Sarcomenia* group in the Rhodomelaceae. In other respects, in the restriction of procarps to one series of transverse pericentral cells, the general form of the cystocarp and the structure of the pericarp (but not its post-fertilization origin) the *Sarcomenia* group is also rhodomelaceous.

(*c*) *Spermatangial Blades*

Spermatangia in the Delesseriaceae are produced on small lateral blades and arise from spermatangial mother cells formed by subdivision of cortical cells. In the Rhodomelaceae the spermatangia are usually formed on the trichoblasts, except in *Euzoniella*, *Bostrychia*, *Lophothalia*, and *Rhodomela*, where they are produced from the pericentral cells of polysiphonous branches (Scagel 1953, p. 11). Otherwise there appear to be no constant differences between the two families in spermatangial development. The *Sarcomenia* group, in species in which spermatangia are known, forms spermatangia on small lateral blades, in general from spermatangial mother cells. These are derived from cortical cells cut off from the lateral pericentral cells or derivatives of the flanking cells. While in most species a residual cell remains after division of the lateral pericentral cells to form cortical cells, in *Platysiphonia miniata* the pericentral cells divide directly into two, each of which divides to form spermatangial mother cells.

Spermatangial blades in the *Sarcomenia* group are distinctive in that the marginal cells (flanking cells or their derivatives) and the transverse pericentral cells remain undivided and play no part in spermatangium formation. The blades thus show a central "midrib" and a margin of undivided cells. In most Rhodomelaceae all pericentral cells take part in spermatangium formation, leaving no sterile cells on the surface, but in *Euzoniella* (Scagel 1953, p. 86, Fig. 17) a situation superficially resembling that in the *Sarcomenia* group is found. Here the spermatangial blade is triradiate, with undivided marginal cells in each of the 3 flanges, which are derived from the 3 pericentral cells of vegetative blades.

The distinctive spermatangial blades of the *Sarcomenia* group are not seen in the Delesseriaceae in general, but the situation and origin of the spermatangia are similar. Spermatangial blades of the Delesseriaceae show more irregular fertile areas, without the distinctive lines of sterile transverse pericentral and marginal cells.

Thus the spermatangial blades help little in showing the affinities of the *Sarcomenia* group, but are uniform and distinctive within the group.

(*d*) *Stichidia and Tetrasporangia*

One of the best distinctions that has been recognized between the Delesseriaceae and the Rhodomelaceae lies in the order of sporangium and cover cell development in the stichidium (Papenfuss 1944). In the Delesseriaceae the tetrasporangium is initiated first from the pericentral (or some other) cell, followed by the 2 cover cells, which only partly protect the sporangium. In the Rhodomelaceae the cover cells are formed first and completely protect the sporangium. The *Sarcomenia* group in this respect conforms with the Delesseriaceae and not the Rhodomelaceae.

In the Rhodomelaceae the sporangia are formed from pericentral cells only, except in the Laurencieae and Chondrieae (Scagel 1953, p. 12). In the Delesseriaceae the sporangia in general arise from cortical cells and not pericentral cells, except in *Claudea*, where both types of cells are involved, and *Vanvoorstia*, where pericentral cells only are concerned (Papenfuss 1937). In *Caloglossa* also the sporangia are cut off in a single layer from the lateral pericentral cells and from successive cells of the cell rows of the second order. The *Sarcomenia* group shows more similarity to the Rhodomelaceae on the origin of the sporangia.

The *Sarcomenia* group was originally separated from the Delesserieae as the tetrasporangia occur in a single layer, whereas they occur in two layers in the latter. With the separation of *Claudea* and *Vanvoorstia* from the *Sarcomenia* group by Papenfuss (1937) this distinction now applies with the exception of *Caloglossa*.

While the distinction of the Delesseriaceae and Rhodomelaceae on the order of sporangium and cover cell development appears generally satisfactory, the relationship of the flanking cells and abaxial and adaxial cover cells may be considered with regard to the possible origin of the *Sarcomenia* type of stichidium.

In the Rhodomelaceae the stichidia nearly always possess 5 pericentral cells, whatever the number of vegetative pericentrals. In most genera only 1 pericentral cell per segment is fertile and these are spirally arranged, but in some (Amansieae, *Rhodomela*, *Odonthalia*) the sporangia occur in 2 longitudinal rows in a flattened stichidium, while in others (*Bostrychia*, *Pleurostichidium*) every pericentral cell of a segment is fertile. The fertile pericentral cell cuts off first 2 or 3 cover cells (which may divide further) and these form a continuous cover protecting the tetrasporangium, which is cut off subsequently from the pericentral cell. In sectional longitudinal view the stichidium commonly shows the fertile pericentral cell with the sporangium anteriorly and the 2 or 3 cover cells laterally (e.g. Fritsch 1945, Fig. 291*G*, *I;* Scagel 1953, Figs. 7*c*, 12*f*).

Such longitudinal views of stichidia with 2 rows of sporangia are strikingly similar to the *Sarcomenia*-type stichidia, the only difference lying in the cells on the abaxial and adaxial surfaces of the stichidium. Whereas in the Rhodomelaceae such stichidia have 2 pericentral cells on one surface and 1 on the other, there is a single abaxial and single adaxial pericentral cell in the *Sarcomenia* type. Further, the fertile pericentral cells of the Rhodomelaceae do not cut off cells on the abaxial and adaxial surfaces comparable to the cover cells of the *Sarcomenia* group.

The usual interpretation of the first-formed derivatives of the lateral pericentral cells of the *Sarcomenia* group as "flanking cells" and the post-sporangial derivatives as "cover cells" derives largely from the presence of similar flanking cells in the vegetative thallus and also in the Delesserieae generally.

It is possible, however, that the flanking cells of the *Sarcomenia* group stichidium should be interpreted as cover cells comparable to those of the Rhodomelaceae, and the abaxial and adaxial "cover cells" as extra cells developed in the *Sarcomenia*-type stichidium to give some protection to the tetrasporangia, which otherwise lie completely exposed owing to the flattening of the stichidium and the presence of only 4 pericentral cells. This is supported by the fact that both the cover cells of the Rhodomelaceae and flanking cells are formed radially to the stichidium axis, whereas the *Sarcomenia* group cover cells are formed by the lateral pericentral cells at right angles to the plane of the stichidium. It is noteworthy also that in *Vanvoorstia coccinea* the "flanking cells" of the stichidium do not form a wing to the stichidium, but act as "cortical cells" (Papenfuss 1937, p. 58) or cover cells similar to those cut off by the 2 abaxial and 1 adaxial pericentral cell, a terete stichidium resulting.

On the basis of this interpretation (the cover or flanking cells being formed before the sporangium), the *Sarcomenia* group stichidium can be interpreted as having been derived from the rhodomelaceous type. Other features of the stichidium, while not conclusive, also resemble the Rhodomelaceae rather than the Delesseriaceae.

The lack of flanking cells in vegetative parts of *Malaconema* and *Dotyella* and their partial occurrence in *Cottoniella arcuata* may also indicate the derivation of the *Sarcomenia* group from rhodomelaceous ancestors.

(*e*) *Conclusions as to the Position of the* Sarcomenia *Group*

The above discussion shows that of the three distinguishing features between the Delesseriaceae and Rhodomelaceae which have been considered most important, two (the order of pericentral cell development and the branching of the gonimoblast) place the *Sarcomenia* group in the Rhodomelaceae and one (the order of sporangium and cover cell development) is apparently similar to the Delesseriaceae but may be derived from the Rhodomelaceae.

Other vegetative features (position of the procarps, presence of flanking cells, lack of trichoblasts, endogenous branching) are more typical of the Delesseriaceae. The wall structure and general morphology of the cystocarp are rhodomelaceous, but the post-fertilization origin of the pericarp is in general delesseriaceous. The spermatangial blades are distinctive for the *Sarcomenia* group but help little in relationships. Other features of the stichidia are rhodomelaceous rather than delesseriaceous.

The *Sarcomenia* group shows so many features which are characteristic of either the Delesseriaceae or the Rhodomelaceae that it must be recognized as forming an intermediate or linking group between the two families. It could be placed as a subfamily, the Sarcomenioideae, of either family or even recognized as an independent family. The majority of features, however, point to its relationships to the Rhodomelaceae, from which it could have been derived, and it seems best to place the Sarcomenioideae as a subfamily of the Rhodomelaceae. All other groups currently placed in the Rhodomelaceae (Scagel 1953, p. 13) comprise a second subfamily, the Rhodomeloideae, within which these groups are probably best ranked as tribes.

The Sarcomenioideae differ from the Rhodomeloideae in the following respects:

(1) Complete lack of typical trichoblasts (also in *Bostrychia* and a very few other species of Rhodomeloideae).

(2) Endogenous branching (also in Amansieae and Lophosiphonieae).

(3) Reproductive organs borne on small thallus branches, not on trichoblasts.

(4) Spermatangial blades flattened, with sterile transverse pericentral cells and flanking cells (or their derivatives).

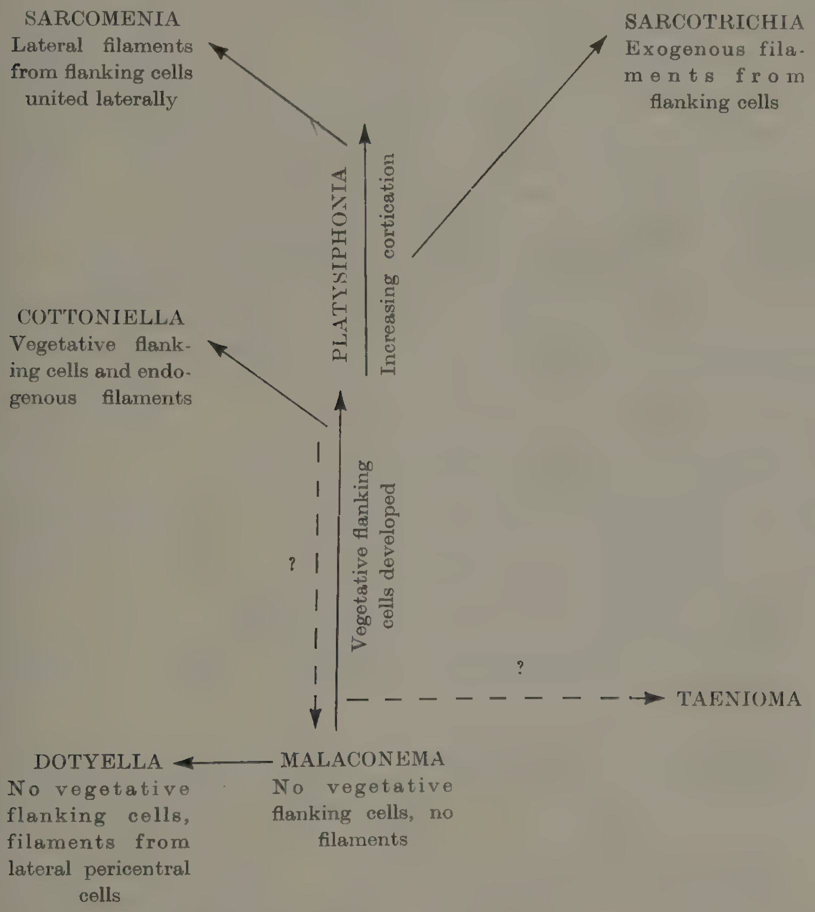
(5) Stichidia with 2 longitudinal rows of sporangia; sporangia formed after the "flanking cells" but before the "cover cells".

VIII. PHYLOGENETIC RELATIONSHIPS OF THE SARCOMENIOIDEAE

The genera of the Sarcomenioideae may be related to each other as expressed in the diagram opposite.

On the basis that the simplest type of structure found in a group usually (but not always) indicates its possible origin, the genus *Malaconema* is of significance. This genus is unfortunately still incompletely known, no female or male plants having been found. Previously it was placed under *Polysiphonia*, as *P. roeana* Harvey. A form such as this could have evolved from a rhodomelaceous alga with 4 pericentral cells by restriction of sporangial production to opposite pericentral cells of a stichidium which had 4 pericentral cells, and by the production of extra cover cells from the stalk cell after sporangium formation. The first-formed rhodomelaceous cover cells would then constitute the flanking cells without significant modification. Associated changes would involve loss of trichoblasts and development of endogenous branching; both these changes occur in some Rhodomelaceae.

It is noteworthy that in most genera of the Sarcomenioideae the cover cells give little protection to the sporangium, especially on the adaxial side. In *Taenioma* neither cover cell protects the sporangium (Papenfuss 1944, p. 207). In the Delesserieae the cover cells are better developed and do protect the sporangium. Actually the curved flanking cells of some members of the Sarcomenioideae give more protection to the sporangia than do the cover cells.


SARCOMENIA
Lateral filaments from flanking cells united laterally
SARCOTRICHIA
Exogenous filaments from flanking cells
PLATYSIPHONIA
Increasing cortication
COTTONIELLA
Vegetative flanking cells and endogenous filaments
?
Vegetative flanking cells developed
?
TAENIOMA
DOTYELLA
No vegetative flanking cells, filaments from lateral pericentral cells
MALACONEMA
No vegetative flanking cells, no filaments

Further developments within the Sarcomenioideae involve:

(1) Spreading of flanking cell development to the vegetative thallus (shown in all genera except *Malaconema* and *Dotyella*, and only partly in *Cottoniella arcuata*).

(2) Further development from the flanking cells or pericentral cells of filaments, usually free (*Sarcotrichia*) but laterally united in *Sarcomenia*.

(3) Increased cortication, especially within the genus *Platysiphonia*.

The possibility that *Malaconema* is a reduced form from a type such as *Platysiphonia*, with loss of vegetative flanking cell development, cannot be excluded.

The position of *Taenioma* is uncertain. This genus differs from other members of the Sarcomenioideae in the apparently delesseriaceous type of pericentral cell formation, in the exogenous branches, and in the restriction of monosiphonous filaments to the apex of determinate branches. Yet the tetrasporangial blades seem to ally *Taenioma* sufficiently with the rest of the Sarcomenioideae to place it in this group. Papenfuss (1944, p. 207), however, considered *Taenioma* to be the simplest of known Delesseriaceae, and further investigations may prove that it is not a member of the Sarcomenioideae.

Papenfuss (1944, p. 210, 211) considers that both the Delesseriaceae and Rhodomelaceae may have evolved from ancestors of the present-day Dasyaceae, and he also agrees with the views of Kylin (1956 and previously) that they represent two parallel lines of evolution, with the Rhodomelaceae somewhat higher than the Delesseriaceae.

The *Sarcomenia*-type stichidium could equally well have evolved from that of the Dasyaceae (which bears several sporangia in each segment, with 2 cover cells cut off after the sporangium) as from the rhodomelaceous stichidium. However, the order of pericentral cell formation sets the Dasyaceae apart from the Rhodomelaceae, and in other features the Sarcomenioideae have more in common with the latter than the former family.

Thus while discussion of the phylogeny of the families of the Ceramiales is very largely speculative, it seems clear that the Sarcomenioideae, while best placed as a distinctive subfamily of the Rhodomelaceae, represents a link between this family and the Delesseriaceae. Further, the stichidium of the Sarcomenioideae could possibly have evolved by reduction of the rhodomelaceous stichidium (with sporangia only from the lateral pericentral cells) and development of extra "cover cells" transversely from the lateral pericentral cells after sporangium formation. The flanking cells would then correspond to the Rhodomelaceae cover cells. Associated changes from the Rhodomelaceae are loss of trichoblasts and restriction to endogenous branching.

In turn the Delesserieae could have evolved from primitive types of the Sarcomenioideae by a change in the plan of pericentral cell formation, to monopodial development of the gonimoblast, and in other less important characters.

IX. Other Genera Possibly Related to the Sarcomenioideae

Other genera that have previously been placed in the *Sarcomenia* group are *Caloglossa*, *Claudea*, *Vanvoorstia*, *Sonderia*, and *Sonderella*. *Caloglossa* is now placed in a group of its own (Papenfuss 1944; Kylin 1956) and *Claudea*, *Vanvoorstia*, and also *Zellera* are placed in the *Claudea* group (Papenfuss 1937; Kylin 1956) of the Delesseriaceae. Papenfuss (Sept. 1956) and Kylin (Oct. 1956) both refer *Sonderia bennettiana* (Harvey) F. Muell. to *Vanvoorstia* as *V. bennettiana*, and *Implicaria reticulata* which Kylin places in the *Claudea* group, has been shown by Segawa (1941, p. 270) to be identical with *Vanvoorstia coccinea*. *Sonderella* is not a member of the Sarcomenioideae and will be discussed elsewhere.

Claudea and *Vanvoorstia* resemble the Sarcomenioideae and differ from other Delesseriaceae in that procarps are formed from only 1 series of transverse pericentral cells (but abaxial in *Claudea* and *Vanvoorstia* while adaxial in the Sarcomenioideae), the cystocarp is urceolate, and the tetrasporangia are formed entirely (*Vanvoorstia*) or mostly (*Claudea*) from pericentral cells. They differ from the Sarcomenioideae in the net formation of the thallus, in the plan of pericentral cell formation in *Claudea* (but not in *Vanvoorstia*), in the formation of sporangia from more than the 2 lateral pericentral cells, and in the pericarp structure, which appears to be more delesseriaceous. The method of branching of the gonimoblast has not been established, though the figures of Papenfuss (1937) indicate that *Claudea* and *Vanvoorstia* may differ in this respect.

Papenfuss (1937) found that the order of pericentral cell formation in *Claudea multifida* is typically delesseriaceous, and he appears to consider the same true of *Vanvoorstia spectabilis* and *V. coccinea*. However, Silva and Cleary (1954, p. 259) state that *Vanvoorstia* follows the rhodomelaceous plan of pericentral cell formation, and this is certainly true of material of *V. spectabilis* from Ceylon that we have examined. However, the adaxial pericentral cell appears to be formed first, in contrast to the abaxial pericentral cell in the Sarcomenioideae. *Claudea elegans* agrees with *C. multifida* in showing the delesseriaceous plan. This appears to be a unique case of two apparently very closely related genera differing in a feature which has been recognized as the best distinction between the families Delesseriaceae and Rhodomelaceae.

Little is known of *Zellera*, but a herbarium specimen of *Z. tawalliana*, from the Malay Archipelago, which we have examined shows formation of the 2 lateral pericentral cells first, while the cell lineages of the blade are similar to those of *Caloglossa* or the *Hypoglossum* group of the Delesseriaceae, i.e. each cell of the chain derived from the anterior flanking cell produces a chain of cells posteriorly, with all tertiary apical cells reaching the thallus edge. The position of *Zellera* is dependent on examination of fertile material, but the net formation derived from anastomosing of 4 orders of blades, and endogenous branching from the central cells, show close affinity with the *Claudea* group.

The *Claudea* group appears to differ significantly from the Sarcomenioideae, though showing some features in common, and is probably correctly placed as a group of the Delesseriaceae.

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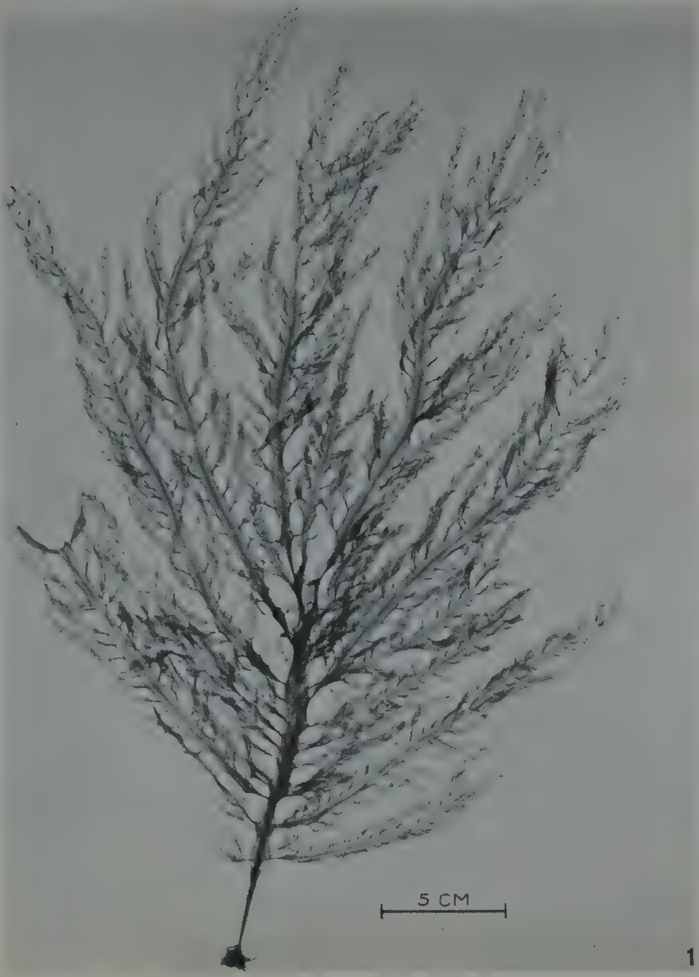
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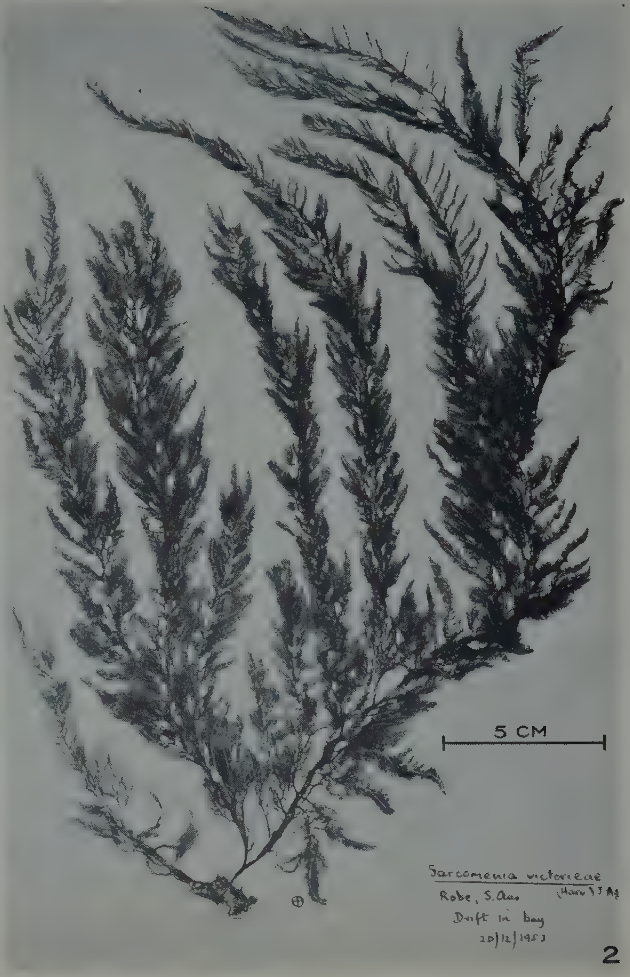
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Robe, S. Aus
Drift in bay
20/12/1953
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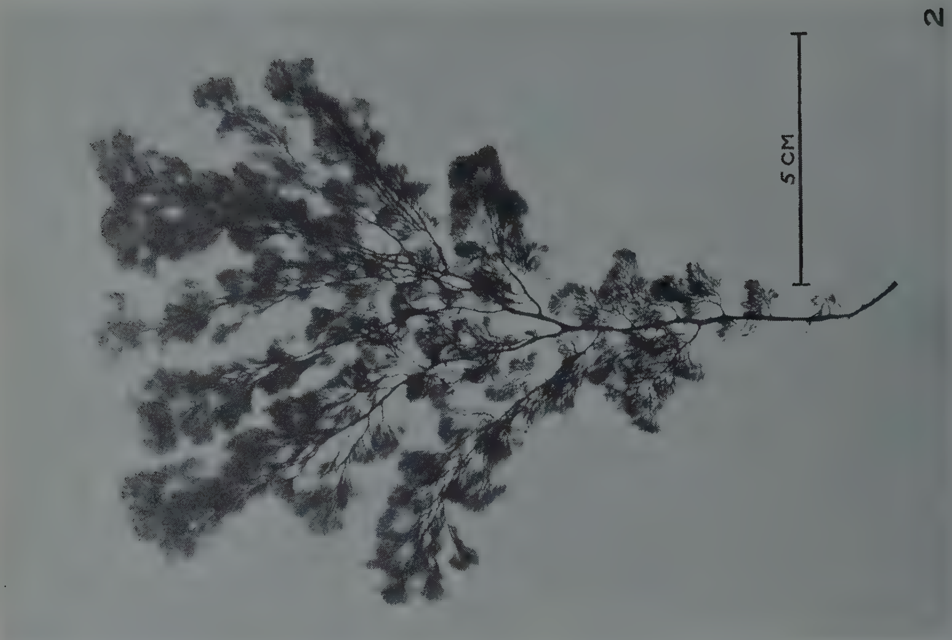
STUDIES ON SARCOMENIA GROUP



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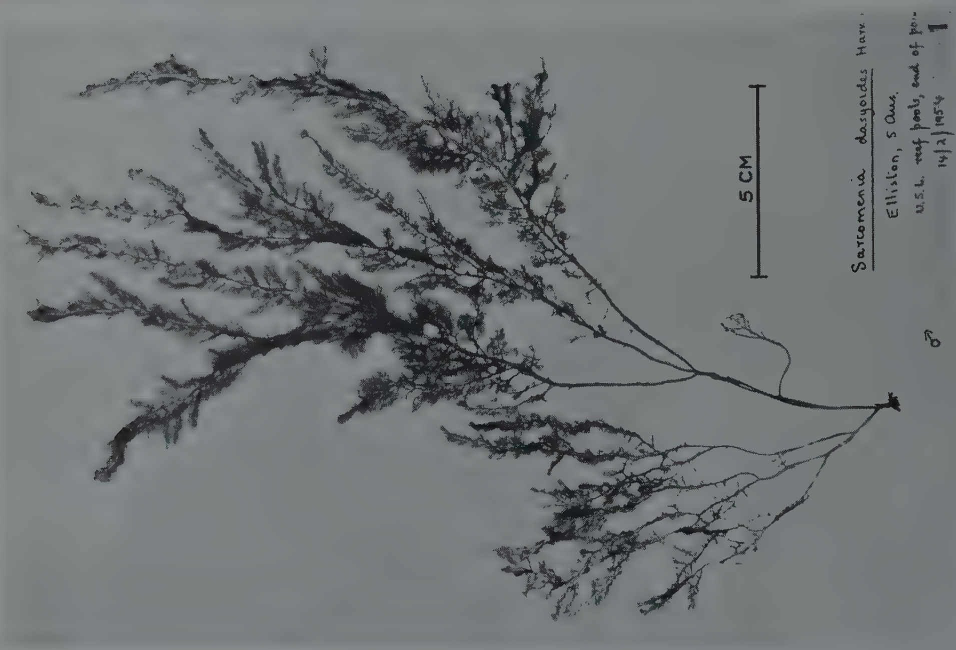
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Elliston, S Aus.
U.S.L. reef pools, end of pt
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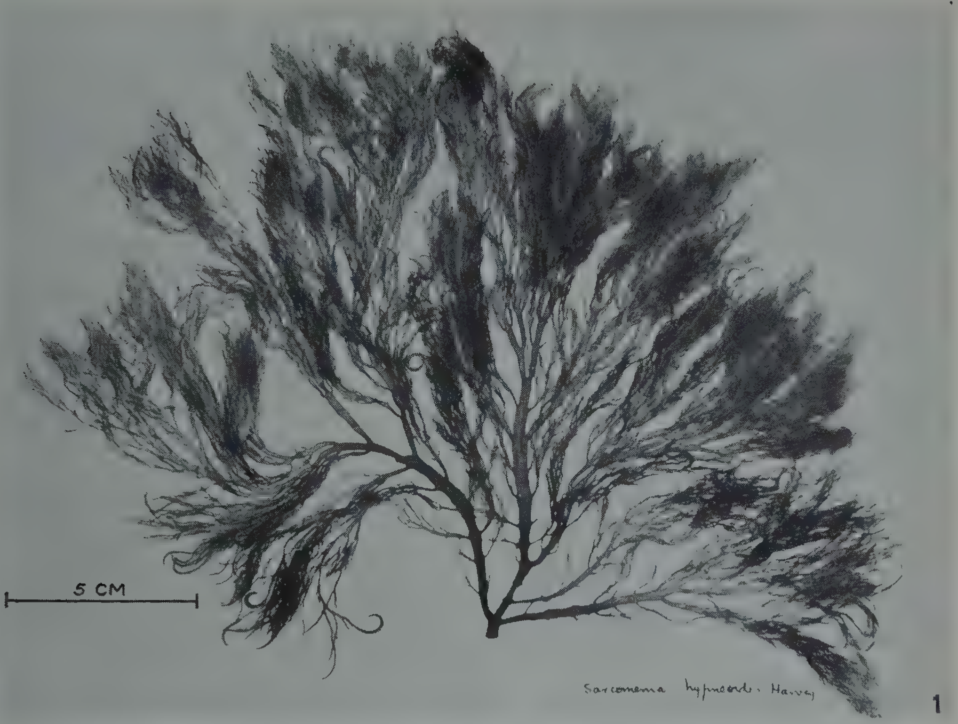
STUDIES ON SARCOMENIA GROUP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Sarcomena hypneoides. Harvey

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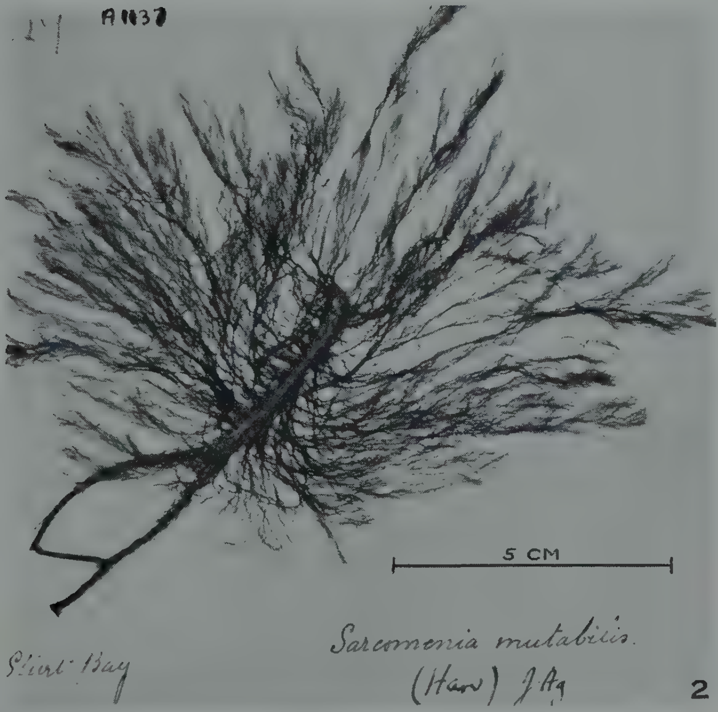
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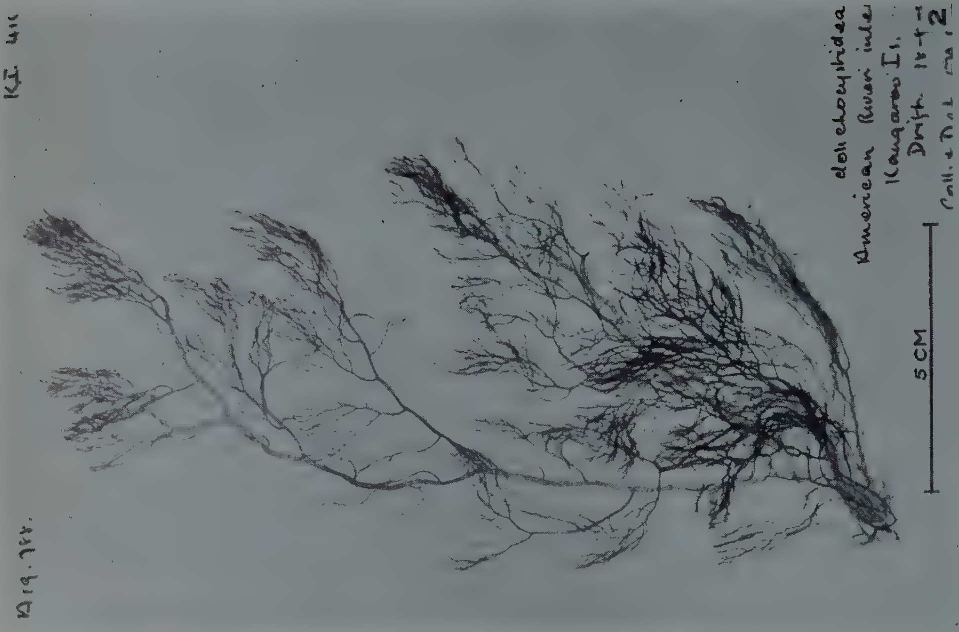
(Harv) J Ag

2

STUDIES ON SARCOMENIA GROUP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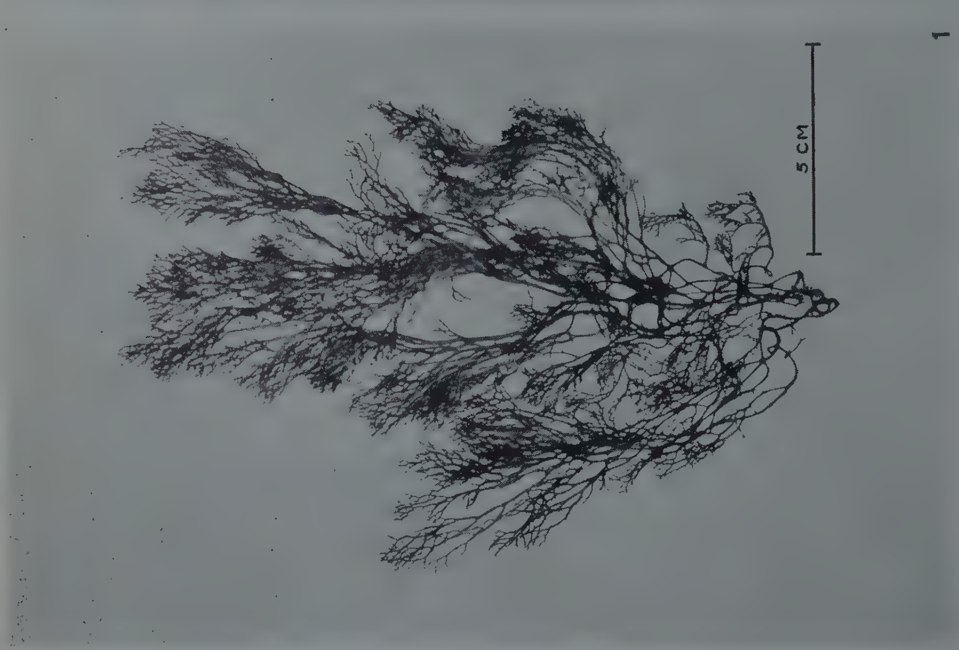

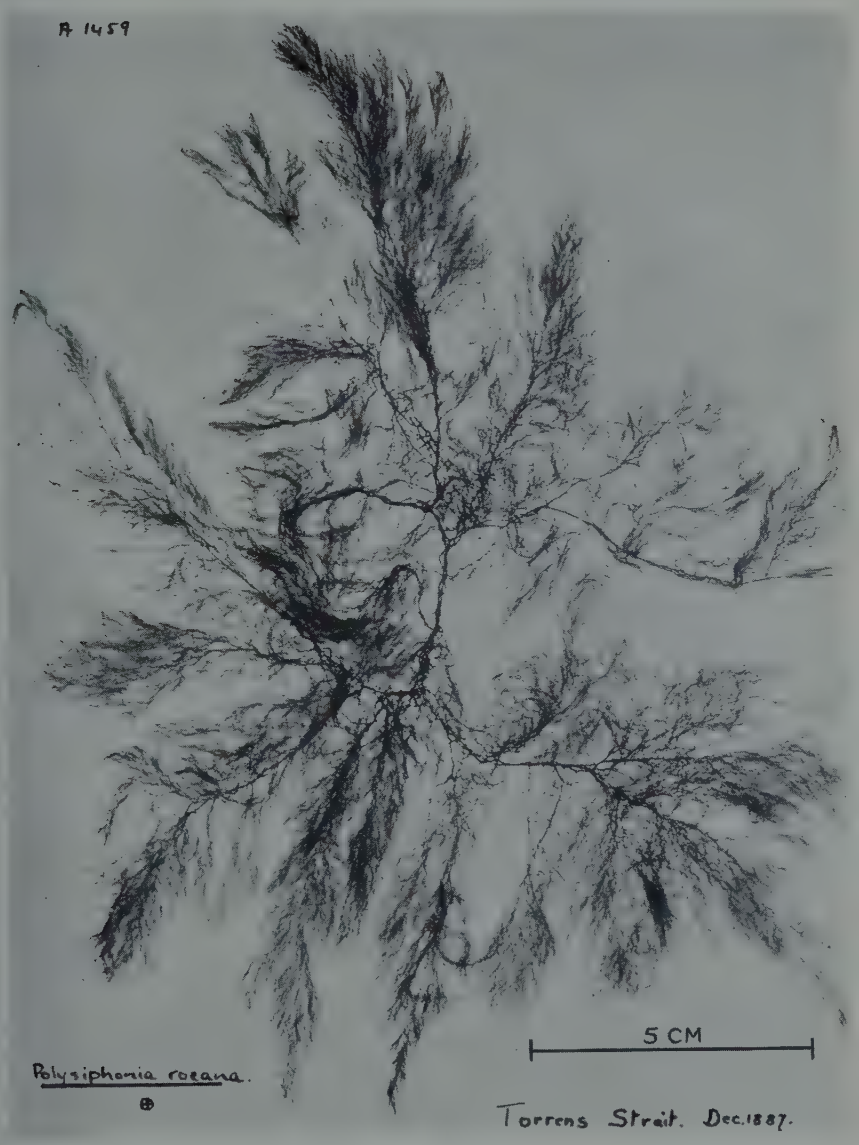

A 1459
5 CM
Polysiphonia roeana.
Torrens Strait. Dec.1887.

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Explanation of Plates 1–5

Plate 1

Fig. 1.—*Sarcomenia delesserioides* Sonder. Robe, S.A. (AD: A19872).

Fig. 2.—*Sarcomenia victoriae* Harvey ex J. Agardh. Robe, S.A. (AD: A19124).

Plate 2

Fig. 1.—*Sarcomenia victoriae* Harvey ex J. Agardh. Reef form (= *S. dasyoides* J. Agardh). Elliston, S.A. (AD: A19423).

Fig. 2.—*Sarcomenia corymbosa* J. Agardh. Port McDonnell, S.A. (AD: A18991).

Plate 3

Fig. 1.—*Sarcomenia hypneoides* Harvey. Western Australia (AD: A18301).

Fig. 2.—*Sarcomenia mutabilis* (Harvey) J. Agardh. Marion Bay, S.A. (AD: A1137).

Plate 4

Fig. 1.—*Sarcomenia tenera* (Harvey) J. Agardh. Marion Bay, S.A. (AD: A16097).

Fig. 2.—*Sarcomenia dolichocystidea* J. Agardh. American River Inlet, Kangaroo I., S.A. (AD: A19788).

Plate 5

Polysiphonia roeana Harvey. Torrens Strait, S.A. (AD: A1459).

GASTRODIA SESAMOIDES R.BR. AND ITS ENDOPHYTE

By Ethel I. McLennan*

[*Manuscript received May* 27, 1959]

Summary

The anatomy of the tuberous rhizome of *Gastrodia sesamoides* R.Br., particularly in relation to the occurrence and detailed structure of its endophyte, is discussed and illustrated. This single Australian species resembles those other species (mainly tropical) that have been described in surviving as a saprophyte by the so-called "digestion" of its fungal symbiont. This takes place in a specialized layer of the cortex, and not, as has previously been thought, by an association with nitrogen-fixing bacteria.

I. Introduction

Gastrodia is a genus of saprophytic orchids with 15 species (Holltum 1953), and a distribution through Malaysia spreading into eastern India and Japan, with its southern extension to New Zealand and Australia. There is only one species, *Gastrodia sesamoides* R.Br., present in Australia. Bailey (1896) described an orchid from the Cairns district of Queensland under the name *Gastrodia ovata*. Schlechter (1911) renamed this form *Cheirostylis ovata* (Bailey) Schlechter, so that there remains but the single Australian species.

G. sesamoides is a leafless plant, perennating in the ground in the form of large brownish swollen stem tubers bearing an occasional long thin root. The apex of the tuber is covered with scale leaves, and as the tuber increases in size these scales become stretched out horizontally and fragmented. A reddish brown flowering axis is borne terminally; it may reach a height of a foot or so, and in exceptional cases it may attain a greater height. It bears sheathing scale leaves which are somewhat crowded at the base but more distant higher on the axis, and it terminates in a raceme of flowers (Plate 1). Many fine rhizomorphic strands adhere closely to the surface of the tuber.

McLuckie (1923) examined the Australian plant and reported that it was a saprophyte living in association with a mycorrhizic fungus and a bacterium. He considered that the fungal hyphae were not digested by the host cells and "therefore function more like an ectotrophic than an endotrophic mycorrhiza". He also stated that "bacteria occur in enormous numbers in the living cells of the rhizomes, sometimes as ovoid colonies or masses surrounded by a gelatinous matrix. Frequently they occur massed in the vicinity of the nucleus or distributed densely throughout the cell". He claimed that these bacteria could fix free atmospheric nitrogen.

The present contribution is concerned with a re-examination of the Australian plant, and establishes the true endophytic character of the mycorrhiza and the absence of bacteria in the host cells.

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II. ANATOMY

The tuber has a narrow protective layer two to three cells thick, consisting of tangentially flattened cork-like pavement cells. The cells of the next two or three outer cortical layers are larger, more or less isodiametric, and bound a layer of larger cells which are intimately associated with the symbiotic fungus. The rest of the tuber in cross section consists of thin-walled parenchyma tissue; scattered through it are typical monocotyledonous vascular bundles. The parenchyma is packed with starch of a characteristic pattern. It is present in the cells in the form of large oval to elliptical aggregate grains, variable in size, with a range of 20–54 by 16–23 μ.

When fresh material is sectioned, a copious milky exudate appears and if this is examined immediately, large and small aggregate grains can be identified in it. After a very short time in water, however, these aggregates break down completely and there are left the individual grains, which show a pronounced Brownian movement and which measure only $0 \cdot 2$–$0 \cdot 3$ μ—the smallest recorded starch granules—the "gelatinous" framework of the larger grains could be seen in the microscope field after their degradation. These granules are grouped by thousands into the large aggregates, and never occur free in the living cells. The addition of iodine to a sample of this exudate gave a pinkish brown colour, and when a sample was heated a colloidal solution resulted. The solid residue obtained after centrifuging some of the exudate followed by a very thorough washing gave, after hydrolysis, a sugar reaction with Fehling's solution. At the same time the supernatant liquid after the last washing gave a negative result. These minute granules, then, show clear "starch" characteristics.

III. THE FUNGUS

Fine rhizomorphic strands closely appressed to the tuber form a network over its surface. The finer of these consist of four or five hyphae running parallel in the strand; numerous clamp connexions are present on the hyphae. Cross sections of the tuber frequently show rhizomorphs cut in section lying between the scale leaves and the outer tuber surface (Plate 1, Fig. 1); the parallel arrangement of the hyphae in the strands is shown by their appearance in transverse view. Individual hyphae can be seen in and between some of the cells of the outer protective layer (Plate 1, Fig. 2), where they branch and force their way into the wall separating a cell of this layer from the isodiametric cell beneath it (Plate 1, Fig. 3). The middle lamella softens and the two cells separate; the cellulose layers become much altered, appear swollen, and take the haematoxylin stain very deeply (Plate 1, Fig. 4). The tips of the hyphae push down into this softened wall, which becomes invaginated; often three or four similar processes are seen in the cell, which appear to be directed towards the nucleus of the occupied cell (Plate 2, Fig. 1). The nucleus becomes enlarged, and highly granular with a very conspicuous nucleolus. In a section through a tuber of 1 cm diameter there are on an average six such penetrated cells, and it is through these individual cells that the fungus gains entrance into the deeper tissues of the tuber. One to several hyphae pass from this cell into the cell or cells immediately beneath. This is often accompanied by invagination of the lower wall (Plate 1, Fig. 3; Plate 2, Fig. 1).

Once into the deeper cell a complex network of hyphae is formed; the neighbouring cells in the same plane are free of the fungus, the penetration restricting itself to the underlying one or two cells; so that two to three layers of the outer cortex, with the exception of the areas of penetration, are free of the fungus (Plate 1, Fig. 2).

Once the tuber has been entered to this depth, tangential extension of the symbiont proceeds by one or several hyphae passing across the lateral walls of the cells, and in each cell entered a similar complex network is formed (Plate 1, Fig. 2). The lateral penetration spreads through three to five cells on either side of the axis of entry. This network is very compact, and examination of the cells in serial sections rarely reveals any sign of a nucleus. Occasionally a cell is found in which a large and deeply staining nucleus persists (Plate 2, Fig. 2). The diameter of the hyphae forming the network is more or less uniform, and the fungal wall appears comparatively thick. The outlines of the hyphae in the cells of this region retain their form throughout the life of the tuber.

Penetration into the limiting layer of fungal infection is gained by one or several hyphae of the network passing through the wall of the cells of the next and deeper layer of the cortex (Plate 1, Fig. 2; Plate 2, Fig. 3). The walls of these hyphae are often thicker than the rest, and invagination of the wall during their penetration is frequent. Immediately entry has been gained the hyphae branch and more delicate hyphal strands are formed which become coiled up like a spring in a most characteristic way (Plate 2, Fig. 4; Plate 3, Fig. 1).

The nucleus has enlarged considerably, and judging from its intensely granular condition it was in a very active metabolic condition (Plate 3, Figs. 1, 2; Plate 4, Figs. 1–3). The fine hyphae direct themselves so that they come into intimate contact with it (Plate 3, Figs. 1, 2). These hyphae then undergo a change (digestion); they swell up enormously (Plate 4, Fig. 1) and eventually stain a deep purple colour, with paler margins when the sections are stained with haematoxylin dyes. Finally large inert masses staining black with Heidenhain's are left in the cell (Plate 4, Figs. 1, 2). At the same time small amyloplastids are seen in the cytoplasm, lying close against the nucleus (Plate 3, Fig. 1; Plate 4, Fig. 3). The rest of the tissue of the tuber remains free of fungal penetration. Attempts to isolate the fungal endophyte have so far not been successful. It is a basidiomycete, for clamp connexions are numerous on the hyphae forming the rhizomorphs.

Kusano (1911), who was the first to examine the cytology of the "infected cells", recorded a symbiotic association between the Japanese species of *Gastrodia* (*G. elata* Bl.) and *Armillaria mellea*. He considered that an inflorescence axis was formed by the tuber only when this association was realized. Burgeff (1932) confirmed the cytological detail for some tropical species: *G. javanica* (Bl.) Sudl., *G. callosa* J. J. Smith, and *G. abscondita* J. J. Smith. McLuckie (1923) described the symbiotic relationship of the Australian species (*G. sesamoides*). He considered that the mycorrhizic fungus was not abundant in the tuberous rhizomes, occurring only in small isolated patches in the outer cells of the ground tissue. He states: "in all the hundreds of cells I have examined there was no suggestion of disorganization or digestion of the fungus by the cell contents". He suggested that the host cells inhabited by the fungus "derive their organic food materials directly from the metabolic processes of the fungus and not indirectly by the digestion and assimilation of its body".

The present work clarifies the position of the Australian species, and shows that the fungus is widespread in the rhizomes and that it undergoes digestion in a particular layer of the cortex. The cytology of this layer is peculiar to the genus and the Australian species forms no exception.

McLuckie also reported the presence of bacteria in the cells of the tubers, and he stated: "the outstanding difference in the nutrition of *G. elata* and *G. sesamoides* lies in the presence of masses of bacteria in the latter and their absence from the former". He emphasized that the bacteria occur in enormous numbers throughout the cells of the rhizome, in the aerial flowering axis, and also in the roots. He reported that the "bacteria" he isolated showed the capacity of nitrogen fixation to a remarkable degree and he considered this as the important phase of the symbiotic relationship. All attempts, made under fully controlled conditions, to isolate *any* bacterial organism from the orchid tissue have proved negative.

It has been shown that when a rhizome is broken across a whitish sap exudes from the cut surface. McLuckie remarked on this and he stated: "a drop of this solution (?) was mounted on a slide and examination revealed the presence of immense numbers of bacteria amongst large spindle-shaped or oval starch grains". These small bodies interpreted by McLuckie as bacteria are in reality very small starch granules showing exceedingly vigorous Brownian movement. Every care has now been taken to determine the nature of these small bodies in the extruded sap, and there is no longer any doubt that they arise by the dissolution of the large starch aggregates which are present in the cells of the tuber. After a few moments in water their disintegration is complete.

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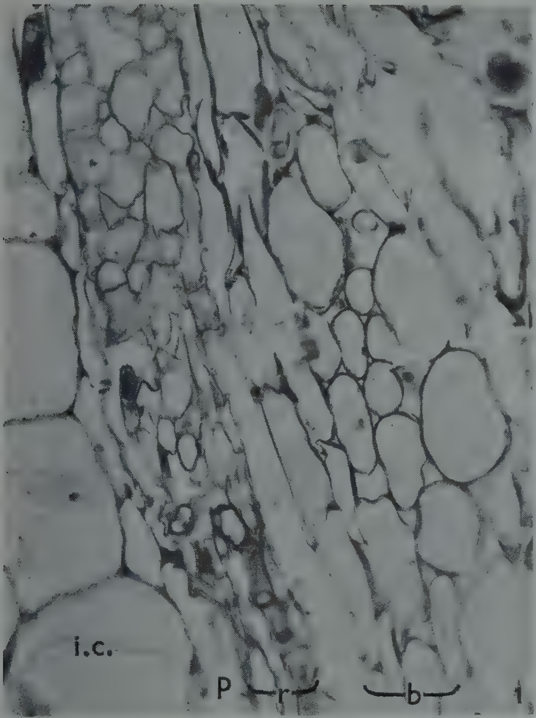
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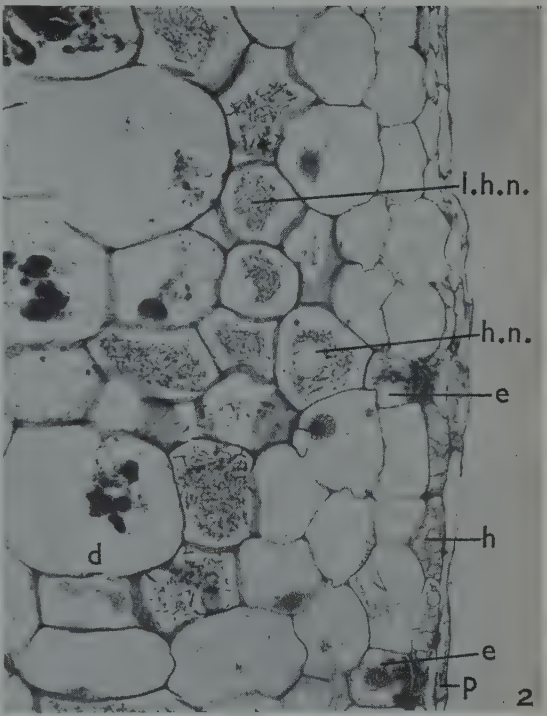
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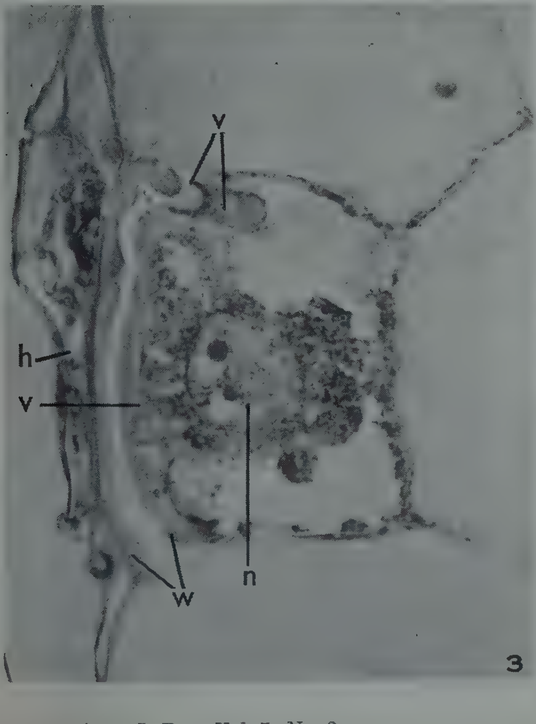
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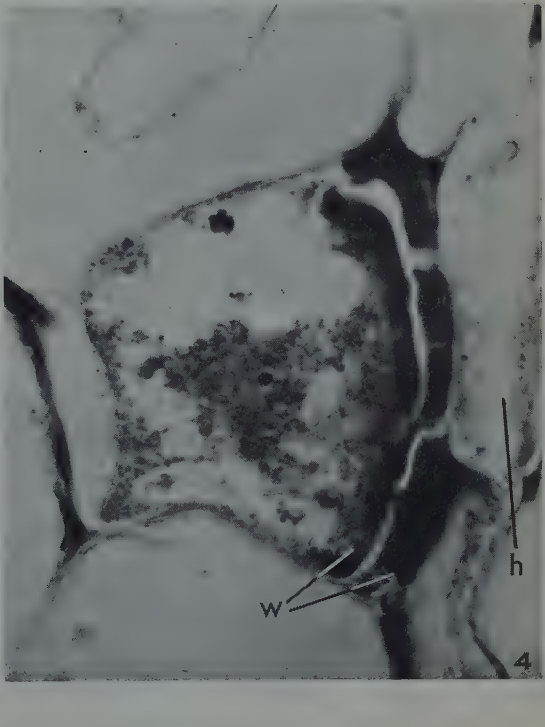
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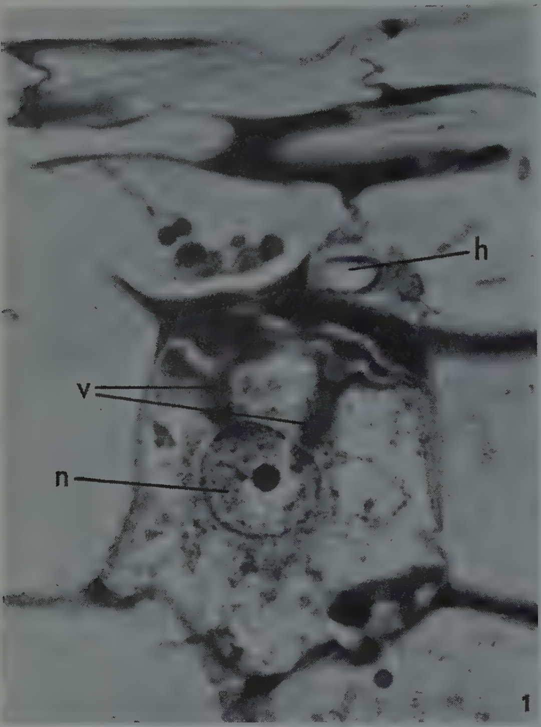
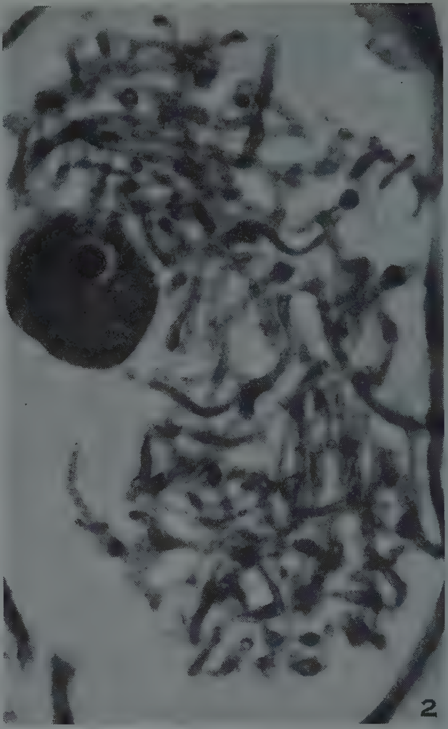
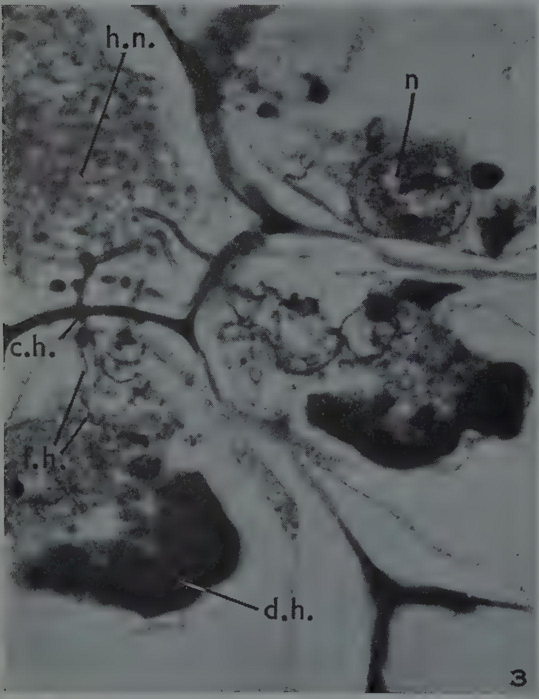
GASTRODIA SESAMOIDES AND ITS ENDOPHYTE



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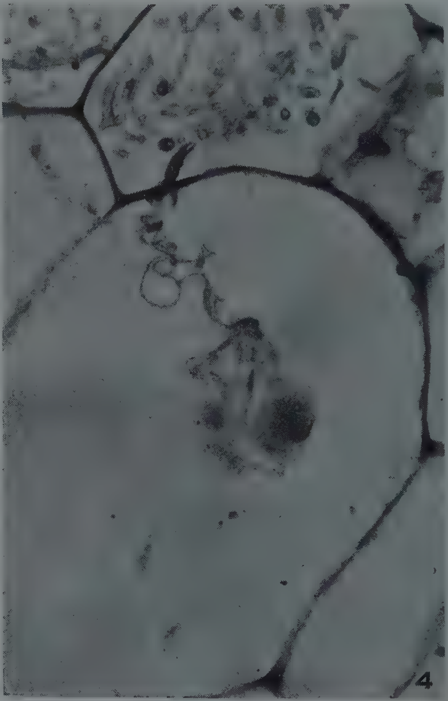

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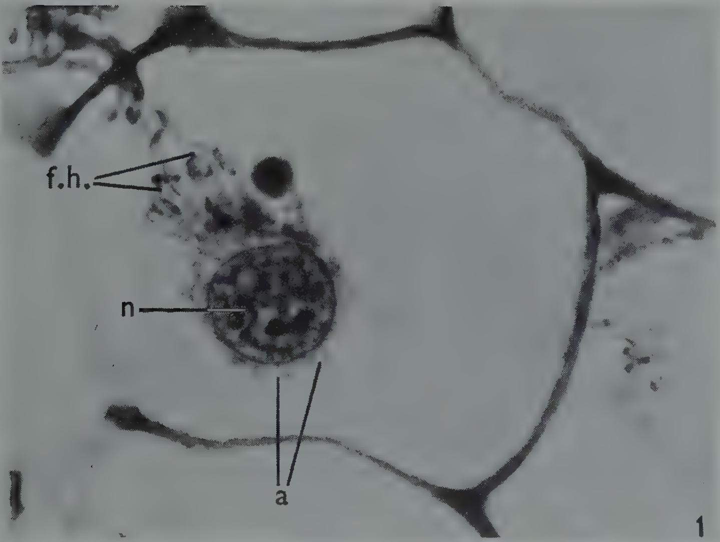

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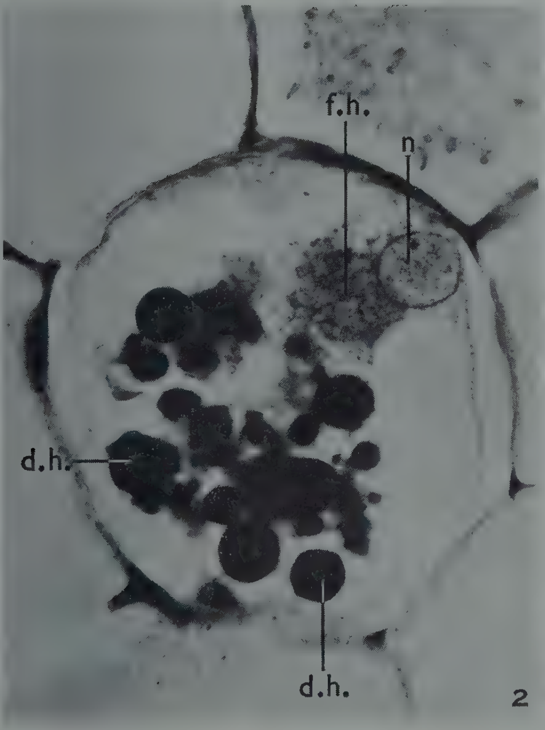

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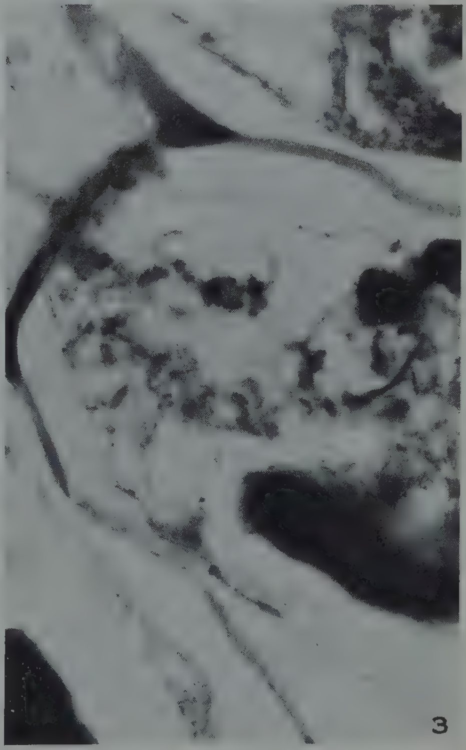

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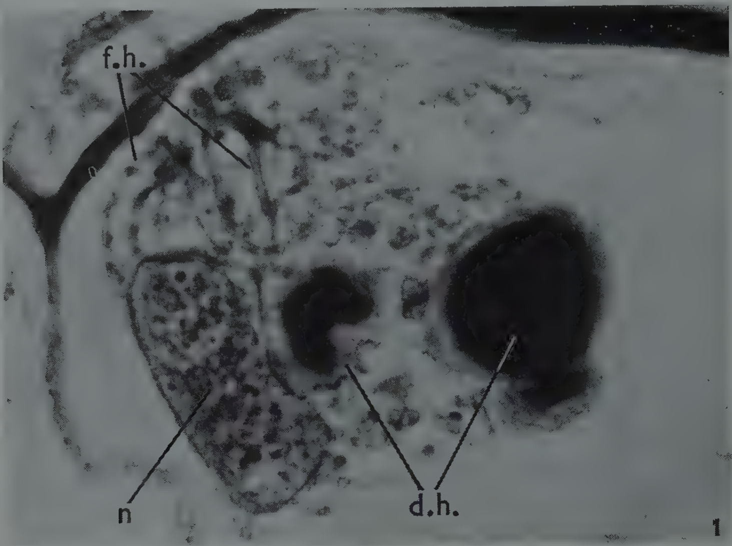
GASTRODIA SESAMOIDES AND ITS ENDOPHYTE



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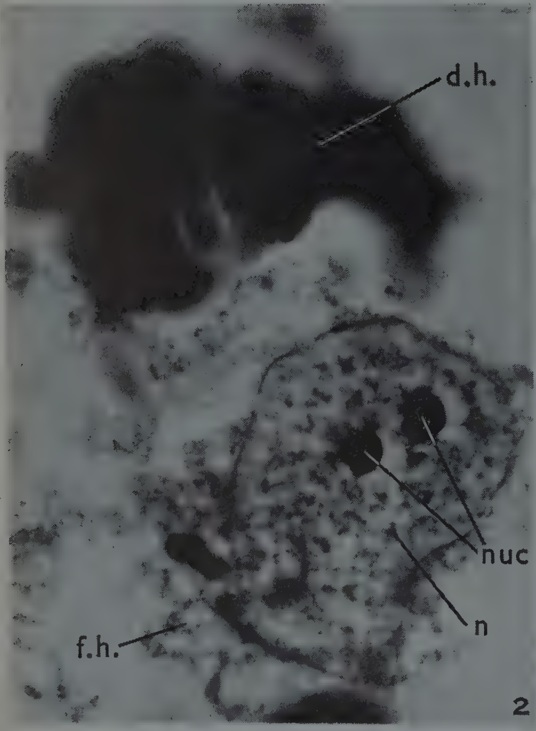

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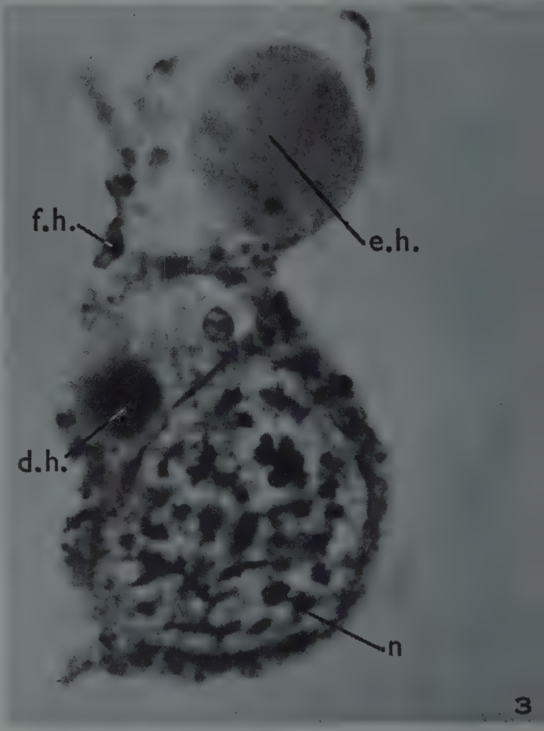

3

Explanation of Plates 1–4

Plate 1

Fig. 1.—Rhizomorph lying between scale leaf and surface of rhizome. ×350. *b*, Cells of scale leaf; *r*, rhizomorphic strand cut transversely; *p*, outer pavement-like suberized cells of stem; *i.c.*, larger isodiametric cells, directly underlying the outer suberized layer.

Fig. 2.—Transverse section through the outer part of the tuberous rhizome to show manner and extent of infection. ×130. *p*, Suberized layer; *h*, hyphae in and between the cells of the suberized layer; *e*, cells through which the fungus gains entrance into the deeper stem tissue; *h.n.*, hyphal network in cell directly beneath entry cell; *l.h.n.*, hyphal network spreading laterally on either side of the point of entry; *d*, cells of digestive zone.

Fig. 3.—A single entry cell. ×950. *h*, Hyphae in cell of suberized layer; *w*, softened wall of entry cell with the swollen cellulose layers separating from one another; *v*, invaginations of wall through which the hyphae pass; *n*, enlarged nucleus.

Fig. 4.—A single entry cell. ×950. *w*, Swollen and deeply stained wall of entry cell; *h*, hyphae in suberized layer.

Plate 2

Fig. 1.—An entry cell showing invaginations of the wall directed towards the nucleus. ×950. *v*, Invaginations of wall; *n*, nucleus; *h*, hyphae in outer suberized cells.

Fig. 2.—A cortical cell with hyphal network, showing nucleus still present in the cell. ×570.

Fig. 3.—Three cells of the digestive zone. ×450. *h.n.*, Hyphal network; *c.h.*, coarse hypha passing into digestive cell; *f.h.*, fine hypal branches arising from it with corkscrew-like outline; *d.h.*, hyphae which have undergone digestion and staining deeply; *n*, nucleus.

Fig. 4.—Single cell of digestive zone to show coiling of the fine branches. ×750.

Plate 3

Fig. 1.—A early stage of penetration of a cell of the digestive zone. ×580. *f.h.*, Fine hyphae directed towards the highly granular nucleus *n*; *a*, amyloplasts appearing in cell in close proximity to the nucleus.

Fig. 2.—A cell showing a later stage of fungal digestion. ×530. *n*, Nucleus; *f.h.*, group of fine hyphae in close proximity to the nucleus; *d.h.*, the deeply staining masses resulting from hyphal digestion.

Fig. 3.—A similar cell. ×750.

Plate 4

Figs. 1–3.—Cells of the digestive zone: Fig. 1, ×800; Fig. 2, ×1000; Fig. 3, ×1400. *n*, Large and highly granular nucleus; *nuc*, nucleolus; *f.h.*, fine hyphae passing towards and around the nucleus; *d.h.*, parts of digested hyphae; *e.h.*, early stage in digestion of hyphae.

CHROMOSOME NUMBERS IN THE CASUARINACEAE

By B. A. Barlow*

[*Manuscript received April* 13, 1959]

Summary

Chromosome numbers of 37 species of *Casuarina* are reported, and found to conform with a suggested division of the genus into major species groups. The extra-Australian species groups are probably ancient, and are at the primary diploid level of the genus ($x = 8$ or 9). Somatic chromosome numbers ranging from 28 to 20 occur in the Australian stocks, and chromosome evolution has possibly involved an ancient polyploidy, followed by stepwise reduction in number. Later evolution in the *distyla* species group has involved no changes in the haploid chromosome number ($n = 11$), but polyploidy within the species has been frequent.

I. Introduction

The genus *Casuarina*, consisting of about 60 species, is an isolated one among the angiosperms, usually being set aside in a separate order, Casuarinales. Owing to a number of unique morphological and anatomical features, the position of the group in the natural system has been the subject of considerable discussion (Treub 1891; Boodle and Worsdell 1894; Hutchinson 1926; Moseley 1948). However, few attempts have been made to assess evolutionary trends within the genus. Two sections were described by Poisson (1871): section *Gymnostomae*, which includes about 15 species distributed in Malaysia, and section *Cryptostomae*, which includes the few remaining Malaysian forms and the 45 (approximately) Australian species. This classification appears to be a natural one, section *Cryptostomae* being the more specialized of the two (L. A. S. Johnson, personal communication). No classification within these sections has been proposed, except that of Bentham (1873) of the Australian species, which is highly artificial. However, section *Cryptostomae* appears to fall into two natural groups, a smaller one which includes the few Malaysian species and a few Australian ones, and a larger one which is entirely Australian (author, unpublished data). These two are here referred to as "group A" and "group B" respectively. A number of morphological characters indicate that the endemic Australian group B of section *Cryptostomae* is the more specialized. One species group stands out in group B because of the morphological similarity of the species, and its consequent taxonomic difficulty. This group, called the *distyla* group, has been revised by Macklin (1927).

A classification of the species on data derived solely from wood anatomy, proposed by Moseley (1948), is based on that of Bentham (1873), but is not consistent with the morphological classification, nor with the cytological observations presented below. The genus is currently under revision by L. A. S. Johnson, National Herbarium, Sydney.

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The 37 species examined cytologically are placed in their respective taxa in Table 2. The forms which have been designated by numbers in the tables are to be described by Johnson as separate species and subspecies.

II. Previous Records of Chromosome Numbers in the Casuarinaceae

Only a few chromosome numbers for species of *Casuarina* have been listed in previous publications, and many of these have not been verified by the present examination (Table 1). The former determinations for *C. stricta*, *C. torulosa*, and *C. equisetifolia* were probably made on incorrectly identified material. The count of $2n = 18$ for *C. montana* (Swamy 1948) is probably the correct one, since it conforms with the number recorded for related species. Other numbers for *C. nana*, *C. paludosa*, *C. littoralis*, and *C. torulosa* from unpublished data of N. Purcell are probably incorrect (cf. Barlow 1958*a*). The material on which Purcell counted $2n = 44$ for *C. distyla* is a distinct species, here referred to as *Casuarina* sp. 3.

Table 1

PREVIOUS RECORDS OF CHROMOSOME NUMBERS IN THE CASUARINACEAE

Species	Previous Determination ($2n$)		Author's Determination	
C. stricta	18	D & J*	26	
	26	D & W†		
C. torulosa	18	D & J	24	(Plate 1, Fig. 2)
	26	D & W		
C. equisetifolia	24	D & J	18	
	18	Swamy 1948		
C. montana	24	D & J		
	18	Swamy 1948		
C. distyla	22, 44	D & W	22	(*C. distyla*)
			22, 44	(*Casuarina* sp. 3)
C. nana	36	D & W	22, 33, 44	(Plate 1, Fig. 5)
C. suberosa (= *littoralis*)	48	D & W	22, 44	
C. paludosa	52	D & W	22, 44	

*Darlington and Janaki Ammal (1945).
†Darlington and Wylie (1955).

III. Materials and Methods

Most of the determinations were made on squash preparations of root tip mitosis in seedlings, stained with orcein, after pretreatment with *p*-dichlorobenzene and fixation in acetic alcohol. A few examinations of pollen mother cell meiosis were made from squash preparations stained with orcein. In most cases the progeny of one or two plants from each locality were examined, although some populations were studied more extensively.

TABLE 2

CHROMOSOME NUMBERS IN CASUARINA

Species	Locality	Chrom. No. ($2n$)	Reference
Sect. GYMNOSTOMAE Poiss.			
C. papuana S. Moore	Lae, New Guinea	16	Plate 1, Fig. 1
	Goroka, New Guinea	16	
Sect. CRYPTOSTOMAE Poiss.			
GROUP A			
C. collina Poiss.	Baie des Pirogues, New Caledonia	18	
C. cunninghamiana Miq.	Lower Portland, N.S.W.	18	
	Near Molong, N.S.W.	18	
	Near Canberra, A.C.T.	18	
C. cristata Miq.	Trangie, N.S.W.	18	
C. equisetifolia L.	Philippines	18	
	Sandakan, North Borneo	18	
C. equisetifolia L. var. *incana* Benth.	Noumea, New Caledonia	18	
	Coff's Harbour, N.S.W.	18	
C. glauca Sieb. ex Spreng.	Long Jetty, N.S.W.	18	
	Warriewood, N.S.W.	18	
Casuarina sp. 1	Goroka, New Guinea	18	
GROUP B			
C. acutivalvis F. Muell.	Wyalkatchem, W.A.	24	
C. campestris Diels	Wialki, W.A.	24	
	Near Northampton, W.A.	24	
C. corniculata F. Muell.	Wialki, W.A.	39	
	50 miles E. of Newdegate, W.A.	39	
C. decaisneana F. Muell.	Mann Range, S.A.	28	
	25 miles SW. of Alice Springs, N.T.	28	
C. decussata Benth.	Pemberton, W.A.	20	
C. dielsiana Gardn.	65 miles E. of Geraldton, W.A.	28	
C. fraseriana Miq.	Perth, W.A.	26	
C. helmsii Ewart & Gordon	Buckleboo, S.A.	24	
C. huegeliana Miq.	Jacup, W.A.	26	
	Darling Scarp, W.A.	26	
C. inophloia F. Muell. & Bailey	Warialda, N.S.W.	24	
C. luehmannii R. T. Bak.	Trangie, N.S.W.	56	
	Near Dubbo, N.S.W.	56	
	Elmore, Vic.	56	
C. microstachya Miq.	Cranbrook, W.A.	20	
C. pinaster Gardn.	Near Newdegate, W.A.	28	
C. preissiana Miq.	Red Hill, W.A.	20	
	Mt. Barren Range, W.A.	20	
C. stricta Ait.	Newport, N.S.W.	26	
	Canberra, A.C.T.	26	
	Near Portland, Vic.	26	
	Near Streaky Bay, S.A.	26	
	Hobart, Tas.	26	

TABLE 2 (*Continued*)

Species	Locality	Chrom. No. ($2n$)	Reference
GROUP B (*Continued*)			
C. thuyoides Miq.	Near Jacup, W.A.	44	
C. torulosa Ait.	Narrabeen, N.S.W.	24	Plate 1, Fig. 2
	Near Port Macquarie, N.S.W.	24	
C. trichodon Miq.	Mt. Melville, W.A.	20	
DISTYLA GROUP			
Casuarina sp. 1	Kenebri, N.S.W.	22	Plate 1, Fig. 3
	La Perouse, N.S.W.	44	
C. distyla Vent.	La Perouse, N.S.W.	22	
Casuarina sp. 3	Cox's Gap, N.S.W.	22	
	Warrumbungle Mountains, N.S.W.	44	
C. lehmanniana Miq.	50 miles N. of Perth, W.A.	22	
	Near Cranbrook, W.A.	22	
C. littoralis Salisb.	See Barlow 1958*a*	22	
		44	
Casuarina sp. 4	Port Davey, Tas.	22	
	25 miles W. of Burnie, Tas.	44	
C. muelleriana Miq.	Mt. Lofty Range, S.A.	22	Plate 1, Fig. 4
C. nana Sieb. ex Spreng.	See Barlow 1958*b*	22	
		33	Plate 1, Fig. 5
		44	
C. paludosa Sieb. ex Spreng.	Near Hall's Gap, Vic.	22	
	Near Mittagong, N.S.W.	44	
G. pusilla Macklin			
subsp. *pusilla*	Kuitpo, S.A.	22	
subsp. 5	Hall's Gap, Vic.	44	
C. rigida Miq.	Near Glen Innes, N.S.W.	22	
C. striata Macklin	Kangaroo I., S.A.	22	

IV. OBSERVATIONS

The chromosome numbers of the species which have been examined are set out in Table 2. In the table the species are placed in their respective sections and groups, as described above, but within these the arrangement of species is alphabetical, except that the closely related species of the *distyla* group have been placed together.

The only chromosome number recorded in section *Gymnostomae* is $2n = 16$ for *C. papuana*. This is the lowest number which has been recorded in the family. The chromosomes are very small, and fairly uniform in size (Plate 1, Fig. 1). The short viability of seeds of species in this section has caused some difficulty in making cytological examinations of related species.

Cytological conditions in the two groups within section *Cryptostomae* are strikingly different. In group A the chromosome number of $2n = 18$ is constant for the six species listed here and *C. montana* (Swamy 1948). The chromosome size is uniform and of the same order as in *C. papuana*. In group B there is considerable variation in chromosome number between species, and diploid numbers range from $2n = 28$ to $2n = 20$. The chromosomes are larger than those of species in group A and section *Gymnostomae*, so that in this family the species group with the higher diploid chromosome numbers also has the larger chromosomes. Within the genomes of most species in group B there is considerable variation in chromosome length, and the ratio of longest to shortest chromosomes may be as high as 4 : 1 (Plate 1, Figs. 3, 4).

The cytological relationships between the species of the *distyla* group have a different pattern from those in the rest of group B. In the *distyla* group the haploid number is constant ($n = 11$) for all species, and polyploidy is of frequent occurrence, tetraploid forms being recorded in most of the species. These conditions contrast with the variation in chromosome number in the rest of group B, and with the low frequency of polyploidy, only three other polyploid species being recorded. These include two tetraploids, *C. luehmannii* ($2n = 56$) and *C. thuyoides* ($2n = 44$), and one species, *C. corniculata*, which appears to be a stable triploid ($2n = 39$). The breeding system of the latter species will be further investigated.

The chromosome numbers and breeding systems in the *distyla* group have been studied in more detail than recorded here, and apomixis has been observed in a number of species. These observations are reported elsewhere (Barlow 1959).

V. Discussion

(*a*) *Basic Chromosome Number*

The chromosome numbers in section *Gymnostomae* and group A of section *Cryptostomae* are the lowest in the family, and are almost certainly diploid numbers. Since these are probably primitive groups, they are apparently at the primary diploid level. The haploid number of *C. papuana*, $x = 8$, may be basic for the family, but examination of other species in section *Gymnostomae* is necessary for verification. The alternative is $x = 9$ of group A of section *Cryptostomae*. The constancy of this number in the group is an indication that it may be a basic one in the family. A basic chromosome number of $x = 12$ has been inferred from previous records, and has been used by Moseley (1948) as supporting evidence for his suggestion that the Casuarinales are derived from the Hamamelidales. This is a secondary number which only occurs in the most advanced species group in the genus.

(*b*) *Chromosome Evolution*

In group A of section *Cryptostomae*, which has representatives outside Australia, differentiation has apparently taken place without changes in chromosome number, even polyploidy being absent. In the endemic Australian group B, in contrast, speciation has apparently been associated with considerable variation in chromosome number, which has probably been in the form of stepwise increase or decrease. The secondary basic numbers of 10, 11, 12, 13, and 14 in group B could be explained either by stepwise increase from $x = 9$, that is, without any polyploidy, or by stepwise reduction from $x = 16$ or 18, produced by polyploidy on $x = 8$ or 9 followed by rediploidization. Because of the reticulate nature of the species relationships in group B, it is difficult to correlate specialization with either the higher or the lower secondary numbers in the series. However, most of the species with $2n = 28$ or 26 are erect trees, whereas most of the shrubby species, which have probably been derived from arborescent ancestors, have $2n = 22$ or 20. The latter hypothesis is thus preferred, and group B may be at a secondary diploid level. The duplication of genetic material by polyploidy would confer a greater tolerance to structural change and loss of chromatin, and may thus have facilitated changes in chromosome number. The variation in chromosome length in the species of this group indicates that translocations, by which means chromosome numbers may be reduced (Tobgy 1943), have become fixed. There have probably been a number of parallel series developed in the group.

These conditions have apparently not been operative, however, in the expansion of the *distyla* group, and the diploid chromosome number has remained constant. Variations have been entirely euploid, and the frequent occurrence of tetraploid forms indicates that there has been a tendency in the *distyla* group for their formation or establishment.

(c) *Historical Significance of the Variation in Chromosome Number in the Family*

Smith-White (1954 and unpublished data) has noted considerable variation in chromosome number in Australian subfamilies and tribes of the Rutaceae, Epacridaceae, and Myrtaceae, whereas these families show general constancy of chromosome number in those subfamilies which occur outside Australia. The Australian groups in these families, like group B of *Casuarina* section *Cryptostomae*, are part of the paleo-Australian element in the flora; that is, they became established in Australia during the first angiosperm invasion of the continent, probably in the late Cretaceous, and have developed in isolation from other continental floras. Smith-White suggests that the low selection pressures which must have operated during the early Tertiary radiation of these groups in Australia permitted survival of aneuploid and structural variants which could not have survived under more rigid selection.

In the tribe Boronieae of the Rutaceae, aneuploid differences in chromosome number are correlated with present-day generic differences. Within the genera these secondary basic numbers are constant, and only euploid variations occur. Smith-White (1954) suggests that stocks which are now recognized as genera were differentiated during the early Tertiary radiation, and show aneuploid differences, but later speciation within these genera has taken place under conditions of high selection pressure, and structural changes have not been tolerated. A response to the formation of unsaturated niches during the later stages of development has been the formation of polyploid forms.

The chromosome numbers in *Casuarina* may be satisfactorily related with this scheme for historical development, and the following events have probably taken place in the history of the genus.

Casuarina originated outside Australia, and evolution in the extra-Australian species groups took place with little variation in chromosome number. A stock entered Australia in the late Cretaceous, and underwent rapid evolutionary radiation in the early Tertiary. Polyploidy and rediploidization produced a secondary diploid level, which was followed by aneuploid changes in chromosome number while low selection pressures operated. As a result forms with chromosome numbers ranging from $2n = 28$ to $2n = 20$ were established. The radiation which produced the *distyla* group took place much later, under higher selection pressures, and without change in basic chromosome number. Tetraploid forms, produced within most of the species, are fairly recent in origin. Since instances of this later development are few, most of the Australian species of *Casuarina* may have been conservative for a considerable time.

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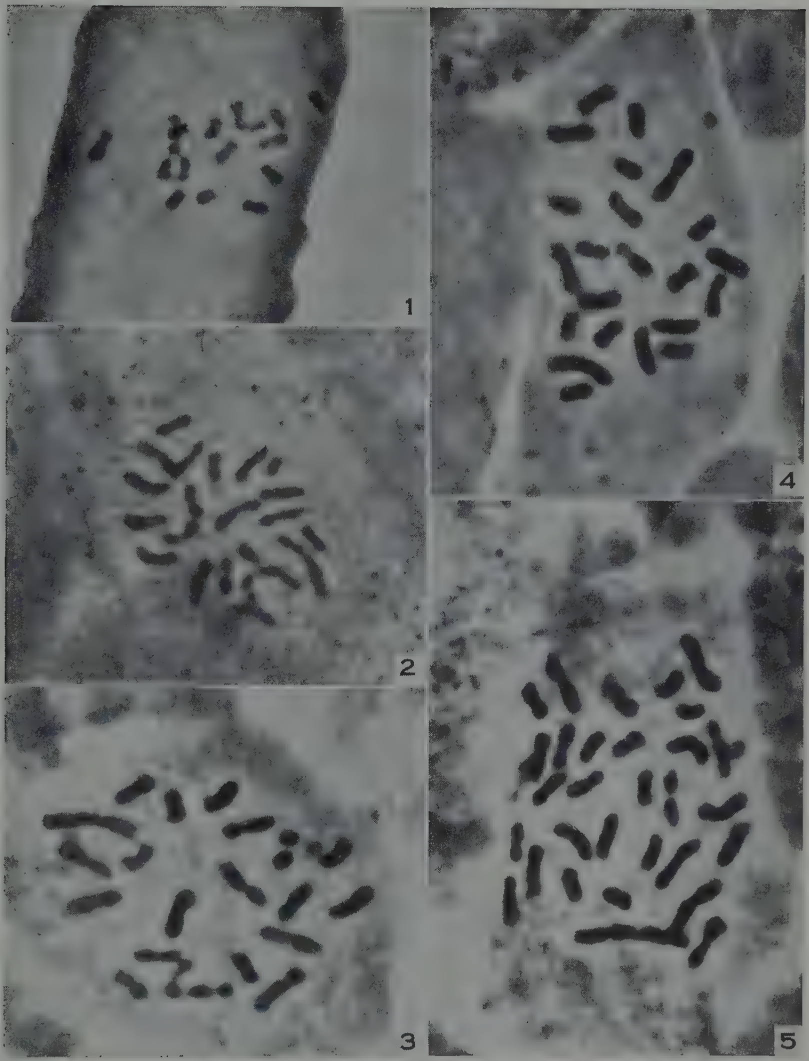

Figs. 1–5.—Root tip mitosis in seedlings of *Casuarina* species. All pretreated with *p*-dichlorobenzene. All ×2500. Fig. 1.—*C. papuana*, $2n = 16$. Fig. 2.—*C. torulosa*, $2n = 24$. Fig. 3.—*C. muelleriana*, $2n = 22$. Fig. 4.—*Casuarina* sp. 2, $2n = 22$. Fig. 5.—*C. nana*, a triploid seedling ($2n = 33$, one chromosome slightly out of focus).

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POLYPLOIDY AND APOMIXIS IN THE *CASUARINA DISTYLA* SPECIES GROUP

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Summary

In the *Casuarina distyla* species group, which includes 13 closely related species, sexual tetraploid forms have been recorded in nine species and apomictic triploids in four. These forms are probably autopolyploids. The triploid apomicts are presumably diplosporous and parthenogenetic, and in two species are pseudogamous, but not in the other two. It is suggested that a transition from the former to the latter breeding system would follow elimination of the need for pseudogamy.

A hypothesis is presented that polyploidy and apomixis have arisen together within the species through establishment in a diploid population of a triploid plant which is diplosporous and parthenogenetic. The genetic system involved probably spread through the group during the evolution of the species, giving them a potential for this kind of development.

I. Introduction

In a recent discussion of chromosome numbers in the genus *Casuarina* (Barlow 1959), it was shown that cytological relationships between the members of the *distyla* species group are different from those between the remaining Australian species. In this group a basic chromosome number of $x = 11$ is constant, and tetraploid forms occur in most species, whereas in the remaining Australian species there is a range of basic or secondary basic numbers, and polyploidy is rare. It was suggested that the *distyla* group has been produced by a fairly recent evolutionary radiation, while most of the remaining Australian species have been conservative.

One member of the group, *C. nana*, is partially apomictic (Barlow 1958*b*). Like most species of *Casuarina*, it is dioecious, and in the partially apomictic populations there is an excess of female plants. Sexual populations may be either diploid or tetraploid, but populations also exist in which there are a few diploids and tetraploids reproducing sexually, and many triploid plants, which are mainly females, reproducing both sexually and apomictically. In the triploid females, embryo sac mother cell meiosis is restitutional, and fertilization by pollen from the diploid results in tetraploid embryos. In addition, synergid parthenogenesis is stimulated, giving triploid embryos, so that the production of heteroploid twin pairs in these plants is frequent. The triploid plants are more vigorous than the diploids and tetraploids. Since the triploids can only reproduce themselves in the presence of fertile (diploid or tetraploid) male plants, an equilibrium frequency of each chromosome form in the population has probably been reached.

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A further cytological examination has been made of the species of the *distyla* group, to obtain information on the relationship between diploid and polyploid forms, and the frequency of occurrence of apomixis. These observations form the subject of the present paper.

The *distyla* group has been taxonomically revised by Macklin (1927) and is currently under revision by L. A. S. Johnson, National Herbarium, Sydney. The forms which have been examined are set out in Table 1. Some forms which are to be described as distinct species or subspecies by Johnson have been designated by numbers, which correspond with those used in a previous paper (Barlow 1959). Material of one undescribed species has not been available for study.

II. Materials and Methods

Most of the observations were made from root tip squash preparations stained with orcein, after pretreatment with *p*-dichlorobenzene. Mitosis in shoot apices, pollen mother cell meiosis, and pollen fertility were examined in some cases. Herbarium specimens have been lodged in the National Herbarium, Sydney, and in the herbarium of the Botany Department, University of Sydney.

Since most of the determinations were made on seedling progenies, it has been necessary to adopt the following principles in interpreting the results.

(*a*) Where all seedlings from a female plant have the same chromosome number, this is presumed to be the number of the parent plant.

(*b*) Where all seedlings from all plants studied in a population have the same chromosome number, the population is regarded as cytologically uniform.

(*c*) If a cytologically uniform population includes male and female plants in approximately equal frequencies, it is considered to be fully sexual; if all or most of the plants are female, it is regarded as being obligatorily apomictic.

(*d*) Where the progenies of some plants are heteroploid, and include heteroploid twin pairs (e.g. triploids and tetraploids), and there is an excess of female plants in the population, a system of diplospory and pseudogamous parthenogenesis, as in *C. nana*, is presumed.

III. Observations

(*a*) *Chromosome Numbers and Breeding Systems*

The chromosomes in species of the *distyla* group are fairly small, and there appears to be no significant difference between species in chromosome size, although within the genomes there is some variation in length (Barlow 1959). A general summary of the recorded chromosome numbers is presented in Table 1, and observations on the breeding systems and distribution of chromosome forms of each species are described separately below. The order in which the species are considered does not reflect any views on natural relationships between species.

(i) *C. rigida*.—No excess of female plants was observed in any of the populations examined, and the species is presumably entirely sexually reproducing at these localities.

TABLE 1

CHROMOSOME NUMBERS IN THE CASUARINA DISTYLA SPECIES GROUP

Species	Localities	No. of Plants Examined	Type of Material Examined	Chrom. No. ($2n$)
C. rigida Miq.	Macpherson Range, Qld.	1	Seedlings	22
	Near Glen Innes, N.S.W.	6	Seedlings	22
	Near Ebor, N.S.W.	1	Seedlings	22
C. lehmanniana Miq.	50 miles N. of Perth, W.A.	1?	Seedlings	22
(= *C. baxteriana* Miq.)	10 miles N. of Cranbrook, W.A.	1?	Seedlings	22
Casuarina sp. 2	Kenebri, N.S.W.	1	Seedlings	22
	Braidwood–Nerriga, N.S.W.	7	Seedlings	22
	30 miles S. of Goulburn, N.S.W.	1	Seedlings	22
	La Perouse, N.S.W.	2	Seedlings	44
Casuarina sp. 3	Cox's Gap–Lee's Pinch, N.S.W.	3	Seedlings	22
	Warrumbungle Mountains, N.S.W.	1?	Seedlings	44
Casuarina sp. 4	Port Davey, Tas.	1	Seedlings	22
	Cradle Mountain Reserve, Tas.	3	Seedlings	22
	Burnie–Stanley, Tas.	2	Seedlings	44
C. paludosa Sieb. ex Spreng.	Hall's Gap–Dunkeld, Vic.	3	Seedlings	22
	Near Heywood, Vic.	1	Seedlings	44
	49 miles E. of Melbourne, Vic.	1	Seedlings	44
	Wonthaggi, Vic.	1?	Seedlings	44
	Orbost, Vic.	1	Seedlings	44
	Goulburn–Mittagong, N.S.W.	3	Seedlings	44
	Near Nerriga, N.S.W.	4	Seedlings	44
	Bulli Plateau, N.S.W.	1	Seedlings	44
C. littoralis Salisb.	See Barlow (1958*a*)		Seedlings, P.M.C.	22, 44
C. muelleriana Miq.	Little Desert, Vic.	1	Seedlings	22
	Near Keith, S.A.	3	Seedlings, P.M.C.	22
	Mt. Lofty Ranges, S.A.	6	Seedlings, shoot apices, P.M.C.	22
	Mt. Hope, S.A.	1	Seedlings	22
	Wilpena Pound, S.A.	5	Seedlings, shoot apices	22
C. nana Sieb. ex Spreng.	See Barlow (1958*b*)		Seedlings, shoot apices	22, 33, 44
C. pusilla Macklin subsp. *pusilla*	Kuitpo, S.A.	1?	Seedlings	22
	Near Keith, S.A. (see Table 2)	9	Shoot apices, seedlings	22
		7	Shoot apices, seedlings	33, 44, 55
subsp. 5	Hall's Gap, Vic.	6	Seedlings	44
	Mt. Compass, S.A.	1	Seedlings	44

TABLE 1 (*Continued*)

Species	Localities	No. of Plants Examined	Type of Material Examined	Chrom. No. ($2n$)
C. striata Macklin	Kangaroo I., S.A.	2	Seedlings	22
	Mt. Lofty Ranges, S.A.	1	Seedlings	22
	Mt. Lofty Ranges, S.A. (see Table 3)	13	Seedlings, shoot apices	33, 55
C. distyla Vent.	La Perouse, N.S.W.	2	Seedlings	22
	Near Katoomba, N.S.W.	1	Seedlings	22
	Near Manly, N.S.W.	3	Seedlings, P.M.C.	22
	Pigeon House Range, N.S.W.	5	Seedlings	22
	Pigeon House Range, N.S.W.	5	Seedlings	33

(ii) *C. lehmanniana*.—The area of *C. lehmanniana* in Western Australia is isolated from those of the eastern species by a migration barrier which has probably been in continuous existence since the Miocene epoch (Crocker and Wood 1947). Although the *distyla* group has undergone a fairly recent evolutionary radiation, it was thus probably well established over a wide area before the middle of the Tertiary period. *C. lehmanniana* is probably relic, and may only occur as a diploid, sexual form.

(iii) *Casuarina* sp. 2.—No excess of female plants has been observed in any of the populations of this species. It is diploid over its area in the tablelands and slopes of New South Wales, but a single population which occurs on coastal sand dunes at La Perouse, giving the species a disjunct distribution, is tetraploid ($2n = 44$).

(iv) *Casuarina* sp. 3.—The areas of the two chromosome forms of *Casuarina* sp. 3 on the northern slopes of New South Wales, and the breeding behaviour, are still insufficiently known.

(v) *Casuarina* sp. 4.—This species occurs widely in Tasmania. The diploid and tetraploid forms may occupy areas of comparable size, the diploid occurring in the central highlands and on the west coast, and the tetraploid on the eastern and northern lowlands. The populations examined are apparently sexual.

(vi) *C. paludosa*.—This species, which has a wide range in the coastal and mountain districts of south-eastern Australia and north-eastern Tasmania, is tetraploid over most of its area. The diploid form has a localized occurrence in the Grampians of Victoria. *C. paludosa* is one of the few species in the genus which are wholly or mainly monoecious. In a few populations it is dioecious, and one of these is at the diploid locality. In these populations male and female plants occur with equal frequency.

(vii) *C. littoralis*.—The wide range of the diploid and tetraploid forms of *C. littoralis* has been discussed previously (Barlow 1958*a*). The tetraploid has an apparently continuous range of 2000 miles in eastern Australia, while the diploid occurs in a number of small areas in New South Wales and southern Queensland. Both forms are entirely sexual.

(viii) *C. muelleriana*.—All of the material of *C. muelleriana* which has been examined is diploid ($2n = 22$). In all populations examined except one, male and female plants were recorded in equal frequencies. At Wilpena Pound, S.A., about 25 plants were examined, and all were cone-bearing. In five of these plants and 80 seedlings in their progeny, the chromosome number of $2n = 22$ was constant. *C. muelleriana* may thus be a diploid apomict at this locality, although alternative explanations are that male plants are present but were not encountered, or that the population is monoecious and was not in flowering season. The suggestion that this population is apomictic may be supported by morphological and cytological data, and is being further investigated.

(ix) *C. nana*.—The occurrence of diploid and tetraploid forms, and of partially apomictic populations including triploid plants, has been described (Barlow 1958*b*).

(x)(*a*) *C. pusilla* subsp. *pusilla*.—This species is a low, compact shrub which occurs in heath country of eastern South Australia and western Victoria. An extensive roadside population a few miles west of Keith, S.A., is characterized by an excess of female plants. The proportion of female plants varies in different parts of the population from about 60 to 90 per cent., but accurate estimation is difficult owing to the occurrence of clonal reproduction by budding from horizontal roots. A number of plants were sampled from the population, and the chromosome numbers of a few were determined from mitoses in shoot apices (Table 2). The results show clearly that the population is mixed, including diploid plants, which are either male or female, and triploid plants, which may be always female. Diploid male plants all have high pollen fertility.

Chromosome numbers of seedling progenies from individual female plants are listed in Table 2. Each plant falls into one of two groups on the basis of the chromosome numbers of its progeny (with the exception of plant No. 585/5·5). The plants in the first group only produce progeny with the diploid number $2n = 22$, and this group includes all those plants for which the number $2n = 22$ has been determined directly from shoot apices. The diploid chromosome form is apparently reproducing sexually and independently of any other chromosome form present. In the second group, which includes two plants found to be triploid, the seedlings are either triploid or tetraploid, and there is a high frequency of heteroploid twins. The breeding system in the population is probably similar to that demonstrated for *C. nana* (Barlow 1958*b*), where restitution in the triploid females results in unreduced embryo sacs, and fertilization by pollen from the diploid produces tetraploid embryos. Parthenogenetic development (probably of synergids) results in triploid embryos and heteroploid twin pairs.

The fate of the tetraploid seedlings is not clear. Since only 12 adult plants have been examined cytologically, the presence of tetraploids in the population in a low but appreciable frequency cannot be excluded. The breeding behaviour of plant No. 585/5·5 can only be explained by assuming that it is tetraploid, as the twin pairs produced were diploid-triploid. One member of each twin pair (the

Table 2

CHROMOSOME NUMBERS OF INDIVIDUAL PLANTS OF CASUARINA PUSILLA SUBSP. PUSILLA, AND THEIR PROGENIES, FROM NEAR KEITH, S.A.

(*a*) *Female Plants*

Plant Number	Chrom. No. (shoot apex mitosis)	Chromosome Numbers of Progeny						
		Single Seedlings				Twin Pairs		
		22	33	44	55	22–33	33–44	33–*c.* 55
588/5·9	*c.* 22	3						
588/7·1	22	4						
588/7·7	22	3						
588/7·8		1						
588/7·9		3						
588/7·12	22	3						
588/7·13	22	5						
585/5·1			3	5	1		2	2
585/5·2			2	3			1	
585/5·3			6	2			1	
585/5·4			5	3			3	
588/6·2							1	
588/7·3	33		1	2			3	
588/7·4	33		4	1			4	
588/5·6	*c.* 33							
585/5·5		1	13	1		2		

(*b*) *Male Plants*

Plant Number	Chrom. No. (shoot apex mitosis)	Pollen Fert. (%)
588/6·3	22	87
588/7·2	22	>95
588/7·5	22	90
588/7·6	22	>95

triploid) would then result from fertilization of a reduced embryo sac, and the other (the diploid) from parthenogenesis in a synergid. The single diploid seedling may have arisen by failure of the triploid member of a twin pair. Most of the progeny were single triploids, which were probably hybrids formed with the more abundant diploids, and only one tetraploid seedling was recorded.

The occurrence of pentaploid seedlings in the progeny of plant No. 585/5·1 necessitates fertilization by diploid pollen, and further indicates the presence of tetraploid males. One seedling, which was classed as a pentaploid, had only 51 chromosomes, and was probably derived from fertilization involving a male gamete with four chromosomes less than a full complement. The low frequency of pentaploid seedlings suggests that the tetraploid male plants may be rare. Possibly they are at a competitive disadvantage against the triploids, as in *C. nana*.

(x)(*b*) *C. pusilla* subsp. 5.—This subspecies is tetraploid at the two localities from which material has been examined. No excess of female plants has been noted, and it is presumed to be sexual. *C. pusilla* subsp. 5 is rather distinct from subsp. *pusilla* in a few vegetative characters, and should perhaps be raised to specific rank. The two forms occupy almost the same area.

(xi) *C. striata.*—In the original description of *C. striata*, Macklin (1927) described both male and female inflorescences but referred to the "scarcity of plants bearing pollen in certain communities". She also stated that monoecious individuals are fairly frequent.

In a number of populations in the Mt. Lofty Ranges, S.A., *C. striata* occurs in mixed communities with *C. muelleriana*, and there is an obvious excess of female plants in these combined populations. Male and female plants of *C. muelleriana* occur with equal frequency, but only female plants of *C. striata* appear to be present. An examination of shoot apex mitoses in three plants of *C. striata* showed them to be triploid ($2n = 33$). Chromosome numbers were also recorded for a number of progenies, and are listed in Table 3. Many of these plants produced triploid seedlings only, but a few pentaploids were recorded, both as single seedlings and in heteroploid twin pairs. The production of triploids in the progenies indicates that reproduction is through parthenogenesis in unreduced embryo sacs, and from the very high frequency it is suggested that fertilization is unnecessary to stimulate parthenogenetic development. However, the observation of four pentaploids, including two in heteroploid twin pairs, shows that some fertilization takes place, and that the male gametes must be diploid. It may be expected that fully sexual tetraploid populations occur, as well as the diploid ones which have been recorded on Kangaroo Island and at an unspecified locality in the Mt. Lofty Ranges.

C. muelleriana occurs as a sexual diploid in these mixed populations. Since tetraploid seedlings were not found in the progeny of triploid *C. striata*, *C. muelleriana* can take no effective part in the reproduction of *C. striata*, and hybridization between the two species is absent or negligible. There is no connexion in breeding system between the two species.

(xii) *C. distyla.*—Over most of its range in the central coast area of New South Wales *C. distyla* is diploid, and the equal frequencies of male and female plants indicate that the species is sexual. A population on the western end of Pigeon House Range, near Nowra, N.S.W., as judged by the examination of over 200 plants, however, consists entirely of female plants. In this population all seedlings from each of five parent plants were found to be triploid. A few pairs of twin seedlings were produced and in each case both members were triploid. The population is apparently diplosporous and parthenogenetic. The absence of embryos produced through fertilization, and the absence of male plants, indicate that pseudogamy is not involved. Less than a mile to the east of this site, male and female plants occur with equal frequencies, and here the species is a sexual diploid one.

(*b*) *Morphology*

Morphologically the polyploid forms in the *distyla* group and their respective diploids are very similar. With the exception of the subspecies of *C. pusilla*, there is at present no way of distinguishing either triploids or tetraploids from their diploid progenitors. Tetraploid plants may in some cases have coarser foliage than the corresponding diploids, but this character shows some variation, and the two forms always widely overlap. In most cryptic forms, such as *Drosophila pseudoobscura* and *D. persimilis* (Dobzhansky 1951) and the *Hemizonia virgata-heermannii-obconica* complex (cf. Stebbins 1950), constant differences in form have been demonstrated after the cytological or reproductive differences have been discovered, and more detailed examination of these *Casuarina* species may reveal constant characteristics diagnostic of particular polyploids. The differences between the subspecies of *C. pusilla* are thus of some significance and strengthen the suggestion that the two may deserve specific rank.

TABLE 3

CHROMOSOME NUMBERS OF PROGENIES OF INDIVIDUAL PLANTS OF CASUARINA STRIATA FROM LOCALITIES IN THE MOUNT LOFTY RANGES, S.A.

Plant Number	Chromosome Numbers of Progeny		
	Single Seedlings		Twin Pairs 33–55
	33	55	
588/1·5	2		
588/1·6	4		1
588/1·9	3	1	1
588/1·13	2	1	
588/3·1	13		
588/4·1	3		
588/9·1	1		
588/9·2	17		
Eichler 14363	1		

IV. DISCUSSION

(*a*) *Hybridization*

Natural hybridization is probably not of frequent occurrence in the group. Even though the species are morphologically similar, they are fairly discrete, and usually show no change in variability where they overlap (e.g. *C. striata* and *C. muelleriana* in the Mt. Lofty Ranges; *C. distyla* and *C. littoralis* at a number of localities in New South Wales). Hybrids which have been reported between *C. distyla* and *C. littoralis* have only been able to survive in disturbed sites (Barlow 1955). The apparent physiological isolation between these two forms may be general throughout the species group. The hybrids between diploid *C. littoralis* and *C. distyla* show perfect chromosome pairing at meiosis, and are as highly fertile as either parent. Since these two species are quite distinct, it is likely that the genomes of all members of the group are structurally similar. Hybridization between diploid forms or tetraploid forms may thus be cytologically undetectable, and chromosomal signs of hybridization may only be available in crosses between diploids and tetraploids.

A few triploids have been recorded in the progeny of one plant of *C. paludosa* ($2n = 44$) where it overlaps the range of *Casuarina* sp. 2 ($2n = 22$) near Braidwood, N.S.W. Tetraploid *C. nana* produces a few triploid seedlings in populations at Pigeon House Range, N.S.W., which may be hybrids with diploid *Casuarina* sp. 2 and *C. distyla* growing nearby, but the species could be hybridizing with its diploid form, although the latter has not yet been recorded in the area (Barlow 1958*b*). Since the species of the *distyla* group frequently occur in small-scale mosaic patterns, especially in the coastal ranges of New South Wales, the paucity of recorded instances of possible cross-fertilization suggests that fairly efficient intrinsic isolating barriers are operating. This suggestion is supported by the reproductive behaviour in triploid *C. striata*, where fertilization may apparently be effected by plants from neighbouring populations, but not by plants of *C. muelleriana* growing in the same population.

(*b*) *Occurrence of Polyploidy and Apomixis*

The occurrence of polyploidy and apomixis in the *distyla* group, as indicated by the principles stated above, is summarized in Table 4. Sexual diploid forms have been recorded in all members of the group, except *C. pusilla* subsp. 5, which has not been extensively examined. Tetraploid forms, which occur in seven species (and probably also in *C. striata*), are sexual. Apomictic triploids occur in four species, and are pseudogamous in two of them. Only in one population of *C. muelleriana* is there a possibility of apomixis at the diploid level.

(*c*) *Development of Polyploid Forms*

The problems of establishment of tetraploid races in dioecious plant species are similar to those in animals, and have been frequently discussed (Stebbins 1950; Dobzhansky 1951). However, in contrast to animals, polyploid series are well known in dioecious and other obligatory cross-fertilized plants. The origin of tetraploidy may occur either by direct somatic doubling, or by a two-stage sexual process, with triploids as intermediates, and both processes may have been involved in the establishment of polyploids in the *distyla* group.

Where sex determination is controlled by strongly dominant male-determining factors on a *Y*-chromosome, as in *Melandrium* (Warmke and Blakeslee 1940), sex determination at the tetraploid level may be stable, with *XXXY* males and *XXXX* females. However, the formation of a dioecious tetraploid form by somatic doubling would require the establishment of two tetraploid plants close together in both space and time, and that one should be female and the other male. The probability of this happening is far lower than the probability of establishment of an hermaphrodite tetraploid, and polyploidy by somatic doubling is probably more frequent when there is a loss of dioecism at the tetraploid level, as in *Empetrum* (Hagerup 1927). Rediploidization and selection back to dioecism may subsequently take place. Such a method may have operated in *C. littoralis* and *C. nana*, where tetraploids are occasionally monoecious, and in *C. paludosa*, where the widespread tetraploid form is extensively monoecious, and the diploid form is dioecious. Among obligatory cross-fertilized plants, an increase in self compatibility with polyploidy has been demonstrated in *Allium* (Levan 1936), and the re-establishment of a self-incompatibility system by selection in a stock in which it has been broken down has been shown in *Petunia* (Mather 1943).

TABLE 4

CHROMOSOME NUMBERS AND BREEDING SYSTEMS IN THE CASUARINA DISTYLA SPECIES GROUP

S, sexual; A, apomictic; Ps, pseudogamous

Species	Chromosome Numbers		
	Diploid $2n = 22$	Triploid $2n = 33$	Tetraploid $2n = 44$
C. rigida	S	—	—
C. lehmanniana	S	—	—
Casuarina sp. 2	S	—	S
Casuarina sp. 3	S	—	S
Casuarina sp. 4	S	—	S
C. paludosa	S	—	S
C. littoralis	S	—	S
C. muelleriana	S, A?	—	—
C. nana	S	A, Ps	S
C. pusilla pusilla	S	A, Ps	S
C. pusilla subsp. 5	—	—	S
C. striata	S	A	?S
C. distyla	S	A	—

Tetraploids may also arise from diploids by a two-stage sexual process, with triploids as intermediates. Triploid plants arise from time to time through non-reduction at gametogenesis, and although this phenomenon would be expected more frequently in hybrids, under some conditions it may be fairly frequent in pure lines (Lewis 1943; Rosenberg 1946). Among allopolyploid forms, *Galeopsis tetrahit* (Müntzing 1936), *Nicotiana tabacum* and *N. rustica* (cf. Goodspeed and Bradley 1942), and many others have been synthesized by this process. Presumed autotetraploids arising in this way have been reported by Powers (1945) in *Parthenium argentatum* and Bergstrom (1938) in apples. Tetraploids in the *distyla* group may have been produced by this stepwise process. Triploid seedlings have been recorded occasionally in diploid populations of *C. nana* and *C. littoralis*, and the occurrence of diplosporous triploids has been indicated in four species of the group. Dioecious species are not placed at a disadvantage in the operation of this method of polyploidy, because a single triploid female plant has the opportunity of producing many tetraploids in an otherwise diploid population. Conditions in the *distyla* group thus indicate that tetraploids could have been formed either by direct somatic doubling or by the two-stage sexual process.

It has been suggested that interspecific hybridization in the group is rare, and since the observed hybrids are highly fertile, this hybridity can cause no greater selection for polyploidy. Irrespective of the method of origin of the tetraploid forms, they have probably arisen in pure diploid populations, that is, they are autotetraploids. These forms are morphologically very similar to their respective diploids, and are probably like the vast majority of autotetraploids in that they could not differentiate into forms which could be described as separate species (Stebbins 1947, 1950). However, arising as they do in an outbreeding group, and perhaps without exact genetic duplication in some cases, they should have sufficient genetic variability to become successful forms, and even increase the range of their particular species. Gustafsson (1947*b*) has emphasized that in natural polyploids fitness is influenced by a number of physiological and generative properties, and by the past history of the diploid ancestors. Competitive inferiority of autotetraploid forms, as suggested by Sakai and Suzuki (1955) from their studies on barley, is not likely to be a feature of autopolyploids in general.

In a previous discussion of chromosome races in *C. littoralis* (Barlow 1958*a*) it was suggested that its tetraploid form is allopolyploid in origin. It is now considered more likely that *C. littoralis*, and all of the other tetraploid forms, are the result of initial autopolyploidy. The tetraploids are highly fertile, and most are probably old enough to have had sufficient time for rediploidization.

(*d*) *Origin and Development of Apomixis and Polyploidy*

The polyploid and apomictic forms which have been recorded do not characterize particular morphological species of the *distyla* group. On the contrary, they occur as conditions *within* the species, and these forms are at present morphologically indistinguishable from their respective diploids. They have probably arisen independently within each species. Polyploidy and apomixis therefore have not been involved in the radiation which has produced this group of species, and species evolution has been entirely at the diploid level. Polyploidy and apomixis have similarly played a subordinate part in differentiation in *Crepis* (Babcock, Stebbins, and Jenkins 1942). The frequent occurrence of polyploidy and apomixis in the *distyla* group must be due to a potential for this kind of development.

The starting point in the development of the complex, partially apomictic populations, as in *C. nana*, is the appearance in a sexual population of a triploid with a capacity for diplospory and parthenogenesis. Such a triploid could arise as a hybrid between pre-existing diploid and tetraploid forms in contact, or could arise in a diploid population either through fertilization involving an unreduced gamete or in the progeny of a spontaneous tetraploid. The potential in the *distyla* group for polyploidy and apomixis is thus expressed in the tendency for triploids to be diplosporous and parthenogenetic. In many new triploids there may be appreciable non-reduction at gametogenesis, but a genetic system would be necessary to stabilize the restitutional behaviour, and would be favoured by mutual selection (Darlington 1956). The action of one or a few genes in causing restitution at meiosis has been demonstrated or suggested, for example, in *Datura* (Satina and Blakeslee 1935), *Parthenium* (Powers 1945), and *Triticum* (Riley and Chapman 1958). The capacity for parthenogenesis is usually determined independently of whether or not there is a factor for diplospory present (Gustafsson 1947*a*). Muntzing (1958) suggests that the ability for parthenogenesis in *Potentilla argentea* may be determined by specific genes. In *Casuarina* there is no evidence that the tetraploids are diplosporous, but occasionally polyhaploids have been recorded in progenies of tetraploid *C. nana* and *C. pusilla* subsp. *pusilla*, so that the capacity for parthenogenesis is probably determined independently of the factor conditioning diplospory.

The potential for polyploidy and apomixis thus may have a genetic basis which is widely distributed as a recessive condition in the diploids of the *distyla* group, but is not present in the rest of the genus. The transmission through the group probably occurred during its early evolution, rather than by hybridization between the present forms. Reasons presented by Powers (1945) as to why apomixis is not likely to appear in the diploids are: firstly, that the tendencies for diplospory and parthenogenesis are not likely to be brought together in a diploid, because plants with the former capacity produce mainly triploid progeny; secondly, that homozygosity for mutant genes is usually deleterious; and thirdly, that incompatibility in diploids would require the development of contemporary strains of pseudogamous apomicts before apomictic populations could develop.

In the *distyla* group, factors other than the actions of specific genes may be important in controlling non-reduction and the subsequent establishment of polyploid and apomictic forms. The apparent absence of apomixis in tetraploids which have arisen from apomictic triploids suggests that the number of genomes present may influence the mode of reproduction. Probably of considerable importance is the long-lived perennial habit of the species concerned, since seed production over a long period of time would increase the prospect of one or a few polyploids or apomicts in an otherwise diploid population giving rise to a new form.

In a mixed population of the *C. nana* type, where the apomictic triploids are pseudogamous, there would be an essential connexion in the breeding system between these plants and the fertile male plants of the diploid (and tetraploid) forms, and the frequencies of diploid, triploid, and tetraploid plants would tend towards an equilibrium. However, if a particular chromosome form gained a selective advantage, mutual selection for a stable independent breeding system in this form would favour its fixation. The triploid apomictic populations of *C. striata* and *C. distyla* have probably been derived in this way. Their breeding behaviour indicates that pseudogamy is not necessary for seed formation, and the transition from a complex reproductive system, as in *C. nana* and *C. pusilla* subsp. *pusilla*, to the simpler, obligatorily apomictic one of *C. striata* and *C. distyla* is probably the result of this single change. In the majority of diplosporous apomicts which are pseudogamous, fertilization of the polar nuclei is essential for endosperm development (Gustafsson 1946), and in *C. striata* and *C. distyla*, as in many other species, the elimination of pseudogamy has probably involved the gaining of a capacity for autonomous endosperm development.

The connexion between polyploidy and apomixis thus shown is that they may be the result of a single phenomenon—a tendency in the group for spontaneously produced triploids in a diploid population to reproduce by diplospory and parthenogenesis. However, the possibility is not excluded that tetraploid forms may also have arisen independently of such a system.

V. Conclusions

(1) The *Casuarina distyla* species group includes 13 closely related species which have probably been produced by a fairly recent evolutionary radiation. The haploid chromosome number of $n = 11$ is constant in the group.

(2) Sexual tetraploid forms occur in eight of the species, and in four species triploid apomicts have been recorded. Since most of the species are dioecious, apomixis results in an excess of female plants in the population.

(3) The apomictic plants in two species occur in mixed populations with sexual plants, and are pseudogamous. In the other two species the apomicts are not pseudogamous, and may occur as pure populations of triploid female plants. It is suggested that a transition from the former to the latter breeding system may take place.

(4) Differentiation of species has taken place entirely at the diploid level. Polyploidy and apomixis have been produced within the species a number of times, but have little evolutionary significance. A hypothesis is presented that polyploidy and apomixis have arisen together in some species through establishment in a diploid population of a triploid plant which is diplosporous and parthenogenetic.

(5) There is apparently a potential in the group for this kind of development. The genetic system involved probably spread through the group during the evolution of the species. The long-lived perennial habit is probably an important factor in this kind of polyploid and apomict formation.

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FACTORS AFFECTING GROWTH AND DISTRIBUTION OF KAURI (*AGATHIS AUSTRALIS* SALISB.)

I. EFFECT OF LIGHT ON THE ESTABLISHMENT OF KAURI AND OF PHYLLOCLADUS TRICHOMANOIDES D. DON

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Summary

A method for determining the effect of light on seedling distribution in the field is described. It can be applied when seedling frequencies are as low as $1/m^2$. The frequency distribution of light intensities occupied by seedlings in a quadrat is compared with the frequency distribution of light intensities measured on a grid in the quadrat. This method was used to study the effect of light intensity on the establishment of two New Zealand gymnosperms, kauri (*Agathis australis*) and *Phyllocladus trichomanoides*, in the nursery community, a semimature *Leptospermum scoparium–L. ericoides* associes. Kauri and *Phyllocladus* did not occur at light intensities below 0·015 and 0·018 full daylight respectively. This limitation appeared to be due to the low light intensity presumably limiting photosynthesis. Kauri, but not *Phyllocladus*, also showed a high light intensity limit, at 0·30 full daylight, above which seedlings did not establish. Reasons are given for considering this as an indirect effect, probably through related solar heating affecting soil temperature or moisture. The optimal light intensity for kauri and *Phyllocladus* seedling establishment was close to the modal light intensity under the *Leptospermum* community: *Leptospermum* spp. were incapable of regenerating under their own cover. These two reasons appear to explain the suitability of the *Leptospermum* community as a nurse crop for the two conifer seedling species.

I. Introduction

(*a*) *General Ecology*

The kauri is New Zealand's finest endemic gymnosperm. The mature tree is particularly impressive, with a great 3–10 ft diameter columnal bole rising up to 150 ft before branching into a massive crown, usually emergent from the forest canopy. Since it was first described by Salisbury in 1807 and by Don (in Lambert's "Pinetum", 1824) there have been many general accounts concerning kauri and kauri forest, summarized by Reed (1953). However, detailed studies have been less common. Cockayne (1908, 1928) and Hutchins (1918, 1919) have given useful descriptive accounts of the forest structure. Recently Mirams (1948, 1951, 1957) studied the various communities of the sere, paying particular attention to the relative abundance of kauri trees of various age groups, together with the factors affecting seed viability and germination. There is little detailed information on the effect of environmental factors on the distribution or structure of kauri forest, though several problems of this type exist. Foremost is the question of the behaviour of kauri seedlings towards low light intensities. Cheeseman (1914) noted that "young kauris are not commonly found in the groves of mature trees. Probably the reason is that the amount of light is not sufficient for the growth of the very young tree". Cockayne (1928) stated that "there are no kauri seedlings in the dense forest . . . *Agathis* is strongly light-demanding . . . being evidently suitable for temporary succession (only)". The need for experimental confirmation of these statements stimulated the present investigations. Other similar problems include the reasons for the preferential occurrence of kauri on ridge tops and its absence from swamps, the southerly limit of distribution at lat. 38° S., the altitudinal limit at approximately 600 m, and the regular occurrence of kauri on poor soil. Many observations suggest that, as with other forest trees (Harley 1939; Bormann 1953; Bourdeau 1954), the controlling phase in the establishment of kauri may be that of seedling establishment. Planted kauri seedlings grow in a variety of environments outside the natural range; for example, 1000 km south of the natural limit, in Otago. The experiments described in this and following papers were therefore carried out to determine the effects of various factors, particularly low light intensities, on kauri seedling growth. For comparison some data have also been collected on the effect of light intensity on the establishment of another indigenous gymnosperm, *Phyllocladus trichomanoides*.

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(*b*) *Light as an Ecological Factor*

For many years there has been an interest in the general effects of light on plant growth and distribution in the field; but until the studies of Blackman and Rutter (1946) the importance of the light factor had not been accurately assessed for a single species. This indicates the difficulty of planning ecological studies in order to separate light effects from associated environmental factors. It is necessary to employ statistical methods, and it was through their use that Blackman and Rutter succeeded. Their method was to lay down a metre grid over the study area, count the number of plants (which ranged from 0 to 80) in a 9 by 9 in. quadrat placed on each grid intersection, and then measure the light intensity at the quadrat centre, the data finally being evaluated by multiple regression analysis. This approach requires high plant densities, *c.* 200/m^2, whereas many forest seedlings, even as seedlings, occur at densities of the order 2–5/m^2. Since the light intensity recorded at the quadrat centre must be representative, it is not possible to increase the quadrat size indefinitely. The maximum size will depend on the degree of uniformity of the light pattern, but could only be 20 by 20 cm to 30 by 30 cm for rain-forest with its heavy undergrowth. Another method is needed which, though less informative, will be applicable to such lower plant densities; this paper reports an attempt to develop one.

The method of measuring the light intensity has a bearing on the statistical approach used, and will be considered first. All intensity measurements were made during shadowless, overcast days so that the light source was completely diffuse. Each intensity was measured relative to that of full unhindered daylight, expressed as a fraction of it, and termed the "relative light intensity", or r.l.i. This is the type of measurement made by Atkins, Poole, and Stanbury (1937) and Blackman and Rutter (1946). The method, unlike one based on absolute units, gives readings which do not vary greatly with the time of day or year. Furthermore, there are no sunflecks to weight the results unduly, so that even under field conditions readings are steady and reproducible, and a spot measurement is as informative as a continuous record. Such measurements are somewhat artificial, in that they are made under one particular condition of the light environment. However, in a dense forest, a large fraction of the light reaching a seedling is diffuse, both because direct sunlight occurs for less than half the total daylight hours (Sapsford 1957) and because a considerable component of the light reaching the floor on a sunny day is diffuse light from sky, clouds, and leaves. Again, the reading, though made in diffuse light, does give a measure of the importance of sunflecks. The intensity of the diffuse light received at any point on the forest floor is largely proportional to the fraction of the overcast sky exposed through gaps in the canopy; similarly in direct sunlight a point is illuminated by a sunfleck while the sun is opposite a canopy gap, and this will occur for a length of time proportional to the percentage of gaps in the canopy. If such gaps are small, numerous, and evenly distributed, and the sun zenith is not low in the sky, the shielding factor will be the same in the two cases. In this way the sun, through its daily and seasonal movements, behaves as a diffuse light source in the shape of a sector biased to one side of the sky. It is because the sector is incomplete and biased that diffuse light and sunfleck measurements do not correspond exactly.

Light colour must also be considered, for the spectral distribution can be affected by cloud conditions, latitude, or absorption by and reflection from the screening leaves (Coombe 1957). On overcast days the first two sources of variation are eliminated as the colour temperature of an overcast sky, 7000°K, is almost constant (Kimball and Hand 1936); but it is more difficult to equate the effects of leaf cover. In the past, too much importance has been placed on those light wavelengths concerned in photosynthesis; it is now known (Wassink and Stolwijk 1956) that plant-light interactions are complex, and that all light wavelengths are important during some phase of growth. However, with reasonable precautions light colour can be ignored in many ecological studies. Allowance must, however, be made for the constantly changing nature of the leaf cover. In deciduous woods the changes are large, and even in evergreen woods they cannot be ignored. It would not be desirable to try to account for a given plant pattern on the basis of a light pattern which had not existed as long as the plant one. Some previous knowledge of the community is needed.

The light intensity of an area (say a quadrat) can be measured by making spot recordings at the intersections of a suitable grid over the area. In this way a sampling method analogous to that of the point quadrat (Goodall 1952) will have been used, and the "population" of light intensities obtained will be a sample of the light intensities occurring in the area; the number of points at a particular intensity, or in a given range, being proportional to the area at that intensity or range. The data so obtained are best expressed in histogram form (Fig. 1), and can be used to compare the light environment in different communities. There has been an unfortunate tendency in the past to attempt to express such a range of light intensities by a single average figure. However, two communities with a similar average can have a very different range and distribution of intensities, and this is ecologically of great importance (cf. Fig. 1).

Data obtained as above are also in a form amenable to statistical treatment. If there is a randomly distributed population of seedlings growing on such an area, and the light intensity at each seedling is measured, then the number of seedlings at a given intensity will be proportional to the area (and hence the number of grid points) at that intensity. However, if light has affected seedling establishment there will be a non-randomness in seedling distribution, which will result in seedlings being under-represented or absent at certain intensities. Comparison of the two sets of readings by a suitable statistical method (variance ratio, t or χ^2 test), should indicate whether or not the differences are significant. This is the basis of the method used in the following investigations. Summarizing, a quadrat is thrown in the vegetation being studied, and a grid of suitable dimensions (e.g. 1 m) is laid down inside. The light intensities are measured, relative to full daylight under overcast (diffusely lit) conditions, at the grid intersections and at every seedling of the species being studied. These intensities are then grouped into 8–10 classes and the ratio (No. of seedlings)/(No. of grid points) determined for each class. Any deviation of the ratio from constancy is examined statistically and interpreted.

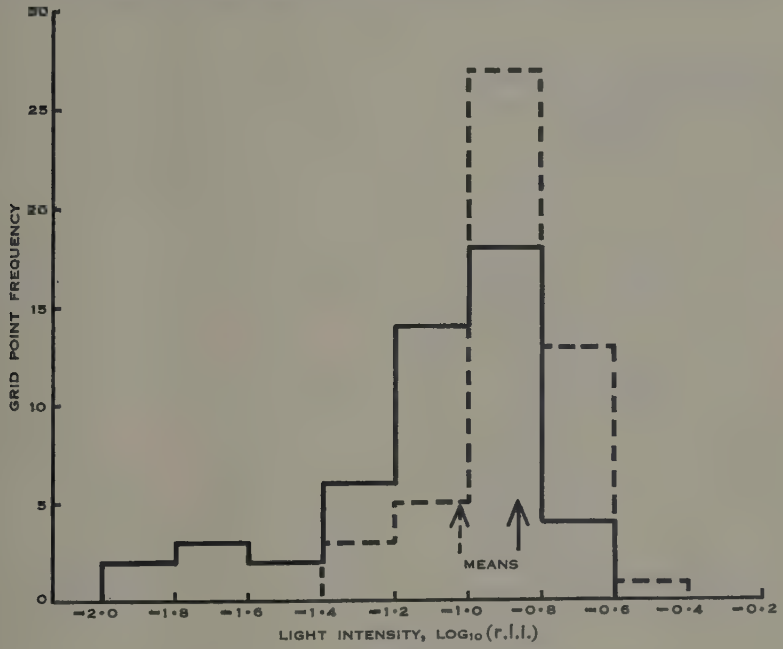

Fig. 1.—The light status of two *Leptospermum* communities, as revealed by the grid point frequency method. - - - - - - Light intensity distribution for a community of stunted, 8 ft *Leptospermum* with little undergrowth. ——— Light intensity distribution for a community of tall, 25 ft *Leptospermum* with little undergrowth. The two show identical modal light intensities and similar mean light intensities, but very different light intensity distributions.

False results are possible. Any factor which affects at the same time both light intensity and seedling establishment would give a false appearance of a dependence of seedling establishment on light intensity, regardless of the statistical approach used. A non-random supply of seed over the quadrat might also give a fortuitous relationship between the two. However, any factors which affect seedling establishment, but which are themselves at random in their action with respect to light, should not produce false results.

II. Methods

(a) Apparatus

The apparatus used for making the light intensity measurements was a portable (24 lb), dry battery–operated, photoelectric cell type, spot-recording light meter,

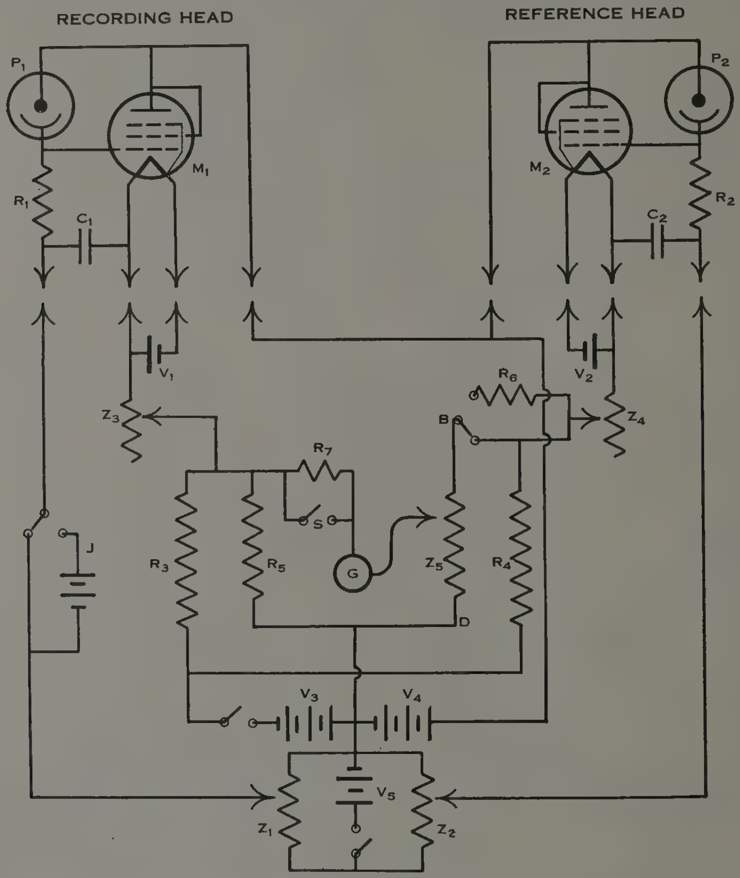

Fig. 2.—Circuit and operation of the portable light-recording meter. *B*, 0·00–0·20 range switch. C_1, C_2, 0·002 μF condensers, tubular, 400 V. *G*, 250–0–250 μA microammeter (as galvanometer). *J*, Standard grid bias, 9 V dry cell battery. M_1, M_2, DL 96 power pentodes. P_1, P_2, R.C.A. 926 phototubes. R_1, R_2, 20 MΩ porcelain resistors. R_3, R_4, 50 K resistors. R_5, 25 K high stability resistor. R_6, 100 K high stability resistor. R_7, 100 K resistor. *S*, Sensitivity press switch. V_1,V_2, 1·5 V dry cell batteries. V_3, V_4, 67 V dry cell batteries. V_5, 9 V dry cell battery. Z_1, Z_2, 100 K wire-wound potentiometers. Z_3, Z_4, 5 K wire-wound potentiometers. Z_5, 25 K wire-wound potentiometer (high quality).

[*For explanation of operation, see opposite page*]

constructed from a circuit (Fig. 2) designed by Dr. F. J. Farley, Physics Department, Auckland University. The light intensity reaching the phototube was controlled to the required level by means of a neutral filter (fogged photographic film); output from the tube was kept high (permitting the use of a more robust galvanometer) yet well below saturation levels. At these light intensities the response of the phototubes was not strictly linear. At the highest light intensities used, the maximum deviation from linearity was —3·0 per cent., while at light intensities one-tenth of this, where neither tube was near saturation, the maximum deviation was —1·5 per cent.

Since the deviation from linearity varied with the light intensity falling on the reference head, errors would be expected. However, under overcast sky conditions, when all field measurements were taken, changes in the reference light intensity over short periods were always less than three-fold. A regular half-hourly check on the reference light intensity was also made, and the correct calibrations used. In this way, the apparatus error was of the order of ±0·25 per cent. full light intensity, and small relative to the other errors inherent in a biological system.

Points of construction are as follows:

(1) The receiving surface of the recording heads was a flat opal glass disk, which, besides being convenient, has the best compromise of characteristics (Atkins and Poole 1930).

(2) The phototube was chosen so that it had a spectral response as similar as possible to that of a plant (cf. Blackman, Black, and Martin 1953).

(3) Electrostatic screening was provided by the metal case of the recording head; this was air-tight and water-tight, contained a silica gel desiccant, and housed all the high resistance components.

(4) The dry batteries used were liable to slight polarization during the course of a day's field work, and therefore the zeroing of the instrument had to be repeated at intervals. Small portable lead accumulators, which are now available, would have been preferable.

Operation of Portable Light-recording Meter

With R_6 out of circuit, both heads are blacked out, and Z_5 is turned to D (the 0·00 r.l.i. position), effectively removing the reference head from the galvanometer circuit. Z_1 is adjusted to zero the dark current from the recording head through G. Z_5 is turned through to B (1·00 r.l.i. position), and Z_2 is adjusted to zero the dark current from the reference head through G. G should now show no deflection in all positions. The two heads are exposed side by side to an even source of light (the open, overcast sky), Z_5 is turned to B, and either Z_3 or Z_4 is adjusted until there is zero current in G. The apparatus is now ready for use in the field. The reference head is fixed so that it is exposed to the unhindered light of the open sky, either by being placed in a cleared area or by being lifted right above the forest canopy. The meter and recording head are carried to the site, the recording head is placed in position, Z_5 adjusted to give zero current in G, and the relative light intensity read off the scale on Z_5. The full scale covers the light intensity range 0·00–1·00 r.l.i.; by switching in resistance R_6 with B, the sensitivity is altered to a full scale of 0·00–0·20 r.l.i. An approximate value for the absolute light intensity falling on the reference head can be obtained by blacking out the recording head, switching J into circuit, adjusting Z_5 to give zero current in G, and reading off the scale on Z_5, previously calibrated against a standard source.

(b) *Field Procedure*

The community studied was the semimature *Leptospermum* community common near Auckland. It has been called the "nursery of kauri", for it generally shelters many kauri seedlings, apparently presenting optimal conditions for their establishment and growth (Cockayne 1928; McKinnon 1930, 1937; Mirams 1957). *Phyllocladus trichomanoides* ("tanekaha"), with which kauri later competes, is common as a seedling in this community, and information was also collected on its behaviour. Care had to be taken to select an area where there had been no animal damage, since cattle and sheep often wander into *Leptospermum* shrubland and break down the undergrowth.

A metre grid was used inside a 6 by 6 m quadrat; this gave 49 grid points and up to 120 seedlings, though experience showed that a 9 by 9 m quadrat with 100 grid points would have been preferable. In laying the quadrat, care was taken to avoid disturbing the thick undergrowth of rush and fern around the quadrat margin, since this would have affected the light intensity. The directions of the sides were established with a prismatic compass; distances were measured by tape (or photographic rangefinder) and a metre rule outside the quadrat and then projected into their true position (Fig. 3). Flags tacked onto long thin sticks were used as markers instead of the usual cords. The reference head of the light meter was seated in an adjustable holder attached to one end of a 12-ft metal pole. This was tied by suitable

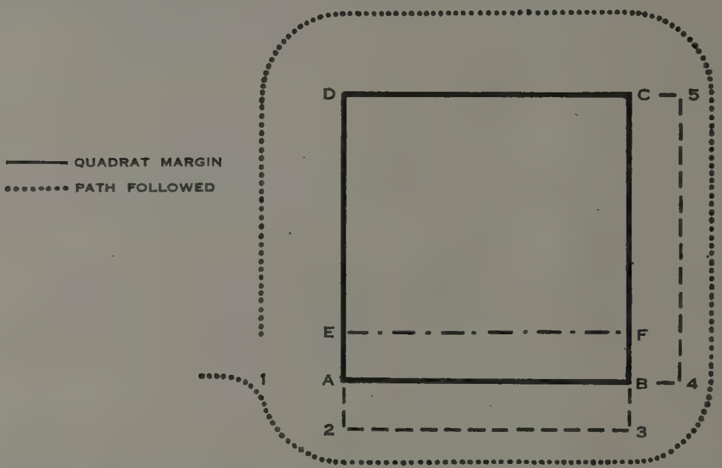

Fig. 3.—Method used to delimit study quadrats. From *1* a flag was fixed at origin *A*, and 1 m measured out to *2*, where a temporary marker was placed. From this, the direction of the side *AB* was established, by compass, through *2* to *3*, 6 m along the line. Direction and distance were checked, then a 1 m perpendicular was measured from *3* to *B*, where a marker was fixed. 1 m was measured along *AB* to *4*, the direction of the side *BC* was established through *4* to *5*, 6 m along the line. The direction and distance were checked, and marker C placed, 1 m from *5*. The quadrat was completed in the same way; another circuit was made to check the quadrat and to insert markers at metre points *E*, *F*, . . . along the sides.

TABLE 1

MEAN LOG_{10} (RELATIVE LIGHT INTENSITY) VALUES, AND SIGNIFICANCE OF DIFFERENCE OF MEANS, FOR QUADRAT GRID POINTS, KAURI SEEDLINGS, AND PHYLLOCLADUS SEEDLINGS IN QUADRATS III, IV, V, AND VI

	Quadrat III			Quadrat IV			Quadrat V			Quadrat VI		
	No.	Mean Log r.l.i.	Mean* r.l.i.	No.	Mean Log r.l.i.	Mean r.l.i.	No.	Mean Log r.l.i.	Mean r.l.i.	No.	Mean Log r.l.i.	Mean r.l.i.
Kauri seedlings	12	−0·978	0·105	67	−0·913	0·122	96	−1·124	0·075	92	−1·240	0·058
Kauri *v.* grid		N.S.†			N.S.			N.S.			5%	
Quadrat grid points	49	−1·098	0·080	49	−0·867	0·136	49	−1·206	0·062	49	−1·334	0·046
Phyllocladus v. grid		N.S.			N.S.			N.S.			1%	
Phyllocladus seedlings	28	−1·063	0·087	25	−0·868	0·135	58	−1·181	0·066	113	−1·177	0·067

*Values computed from antilog (mean log r.l.i.), not arithmetic means.

†Significance of difference of means: N.S., not significant ($P>0\cdot05$); 5%, significant at 5 per cent. level ($P<0\cdot05$); 1%, significant at 1 per cent. level ($P<0\cdot01$).

TABLE 2

VARIANCE OF DISTRIBUTION OF LOG_{10} r.l.i. VALUES, AND SIGNIFICANCE OF DIFFERENCE OF VARIANCE, FOR QUADRAT GRID POINTS, KAURI SEEDLINGS, AND PHYLLOCLADUS SEEDLINGS

	Quadrat III		Quadrat IV		Quadrat V		Quadrat VI	
	D.F.	Variance $\times 10^4$	D.F.	Variance $\times 10^4$	D.F.	Variance $\times 10^4$	D.F.	Variance $\times 10^4$
Kauri seedlings	11	386	66	162	95	417	91	457
Kauri *v.* grid		5%*		5%		1%		1%
Quadrat grid points	48	840	48	263	48	1113	48	975
Phyllocladus v. grid		5%		5%		1%		N.S.
Phyllocladus seedlings	27	413	24	124	57	504	112	741

*Significance of difference of variance values: N.S., not significant; 5%, significant at 5 per cent. level; 1%, significant at 1 per cent. level.

lugs to the top of the tallest tree (preferably a conifer) near the site, so that the top of the pole bearing the reference head extended well above it, and above the forest canopy. The head was then adjusted to horizontal by attached cords. In this way it was exposed to the open sky without the need otherwise for having a large clearing near the sample plot (cf. Blackman and Rutter 1946). The quadrat was covered a square metre at a time, starting at one corner of the quadrat. The recording head was used to measure light intensities at the four corners of the square metre (the grid points) and also at any spot where a seedling was found. Each intensity was recorded in position on a quadrat plan, with a note of the age and species of the seedling. In this way, no undergrowth in an area was damaged until after all records for that part had been taken. Notes were made on the chart of the atmospheric conditions, the quadrat slope and aspect, and the vegetation type and species composition of the undergrowth. Any observable plant pattern was sketched over the top of the quadrat plan.

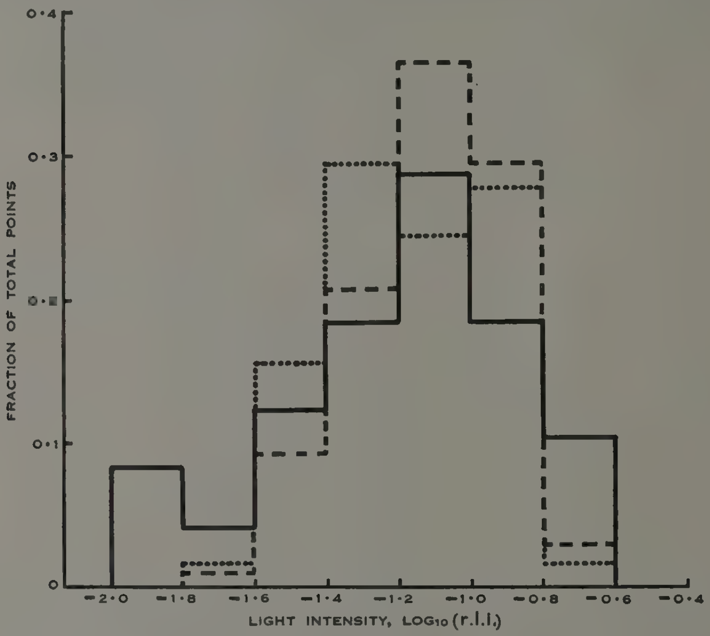

Fig. 4.—Histogram plot of relative frequency of quadrat grid points, kauri seedlings and *Phyllocladus* seedlings at different light intensities in quadrat V. ——— Quadrat grid points. - - - - - - Kauri seedlings. . . . . . . *Phyllocladus* seedlings.

Only young seedlings were studied. The leaf cover in the evergreen *Leptospermum* community slowly changes with time; nevertheless, for seedlings younger than about 2 years it seemed probable that the light climate had not changed significantly. Any change which occurred might have obscured a real relationship between seedling occurrence and light intensity, though it would not have produced a false one. The age of a kauri seedling could nearly always be determined from the number of winter-resting bud scars. Age determination was more difficult with *Phyllocladus*.

All light intensity readings have been expressed on a logarithmic base, since their distribution approximates more closely to a normal curve than when the arithmetic base is used (cf. Bray 1958; Brown 1958). Values thus quoted are $\log_{10}$ (measured light intensity/full daylight (reference) intensity); that is, $\log_{10}$ (relative light intensity), or $\log_{10}$ r.l.i.

III. Results

(a) *Quadrat and Seedling Light Distribution Patterns*

Eight quadrats were completed, and though seedling numbers in four of these were too low to make analysis worth while, their data provided useful information on the light intensity pattern in the *Leptospermum* community. Results from the remaining quadrats are summarized in Table 1. Data from quadrat III have not been used in statistical analyses because of the low number of kauri seedlings present. Except in quadrat VI the differences in mean light intensities are not statistically significant. Kauri seedlings must occur within the range of available light intensities in the quadrat; and if optimal establishment occurred at the modal light intensity for the area, the means would be very close, even though the distributions could be quite different. The distributions can be compared by a variance ratio test (Table 2). The results indicate that the seedlings were found in a range of light intensities significantly narrower than that available in the quadrat area. A histogram plot of the data (Figs. 4, 5) revealed that the seedlings were less common at the lowest light intensities, the same pattern being obtained for all quadrats.

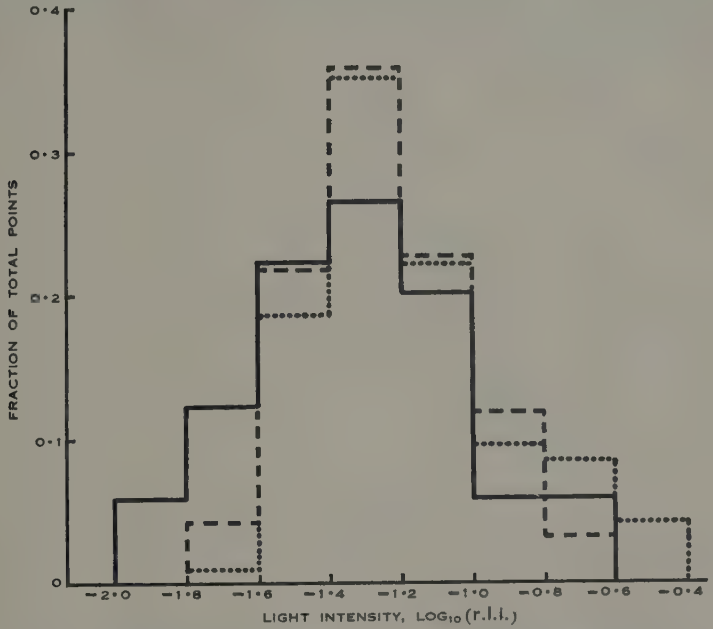

Fig. 5.—Histogram plot of relative frequency of quadrat grid points, kauri seedlings and *Phyllocladus* seedlings at different light intensities in quadrat VI. ——— Quadrat grid points. - - - - - - Kauri seedlings. .... *Phyllocladus* seedlings.

To make a statistical comparison of the number of seedlings *v.* the number of grid points at each range of light intensities, it was necessary, because of the small number of grid points, to combine the data for the various quadrats. This could have been done either by considering each quadrat as an individual and averaging the means, or by assuming that each quadrat was part of one larger sample and grouping the data. The latter method was used because it was more amenable to statistical treatment, it being considered legitimate to lump data from quadrats IV, V, and VI, since they were all within one even-aged community. The conclusions drawn have been shown to apply equally when results were treated ("weighted") to give the same apparent seedling number for each quadrat. It was found that light intensity had strongly influenced the distribution of the two species (Figs. 6, 7). Kauri seedlings did not occur at light intensities lower than —1·84 log r.l.i. (0·014 full daylight) or higher than —0·52 log r.l.i. (0·303 full daylight), showing optimal establishment in the region —1·40 to —0·95 log r.l.i. (0·04–0·12 full daylight). *Phyllocladus* seedlings did not occur at light intensities below —1·74 log r.l.i. (0·018 full daylight), were not limited at high intensities, and showed optimal establishment at —1·38 log r.l.i. (0·042 full daylight). The relative distributions of the two species were compared by the same method; relative to kauri, *Phyllocladus* establishment was significantly higher in the range —1·68 to —1·22 log r.l.i. (0·021–0·060 full daylight), significantly lower in the range —1·22 to —0·79 log r.l.i. (0·060–0·162 full daylight), and considerably and significantly higher at intensities above this.

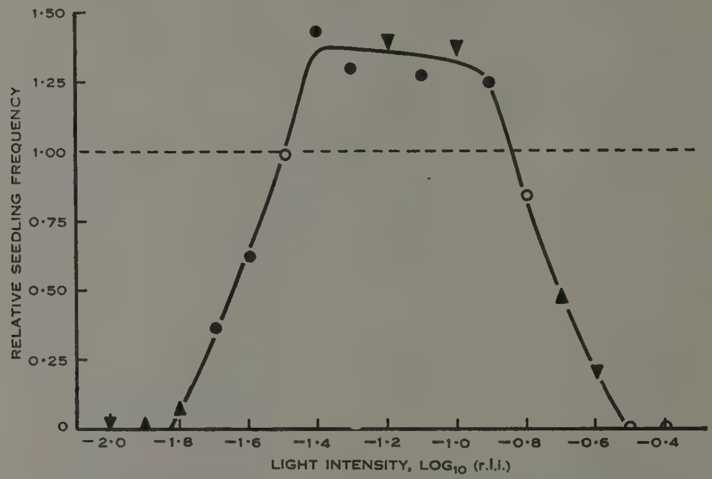

Fig. 6.—Relative frequency of kauri seedlings at various light intensity ranges. Data combined from quadrats IV, V, and VI. Each point gives the value of the ratio:

$$\frac{1}{K}\cdot\frac{\text{No. of seedlings}}{\text{No. of grid points}},\ \text{where } K=\frac{\text{total No. of seedlings}}{\text{total No. of grid points}},$$

for the light intensity range (plotted intensity $\mp 0 \cdot 10$). Significance of deviation of each ratio from the expected value (1·0) has been calculated by a χ^2-test; shown by: ○ $P>0\cdot05$; ● $P<0\cdot05$; ▼ $P<0\cdot01$; ▲ $P<0\cdot001$.

(*b*) *Seedling Age and Distribution Pattern*

The kauri seedling data from quadrats IV, V, and VI were separated into three groups, depending on the age of each seedling. For each age group, the variance of the distribution with respect to light intensity was calculated (Table 3). It was found that there was an increase of variance in the older age groups. Assuming that seedlings from successive years behaved similarly and that there were no marked changes in factors such as soil conditions over the previous 3 years, the most probable explanation seems to be that the plant cover (and hence the light environment) changed during the growth of the older seedlings, which resulted in the variance of the seedling distribution trending towards that of the quadrat. This in turn suggests that, although kauri seedlings became established in a small range of light intensities, they were able to tolerate subsequent changes in the light environment. The group means show that this range extension occurred mainly into the higher light intensities.

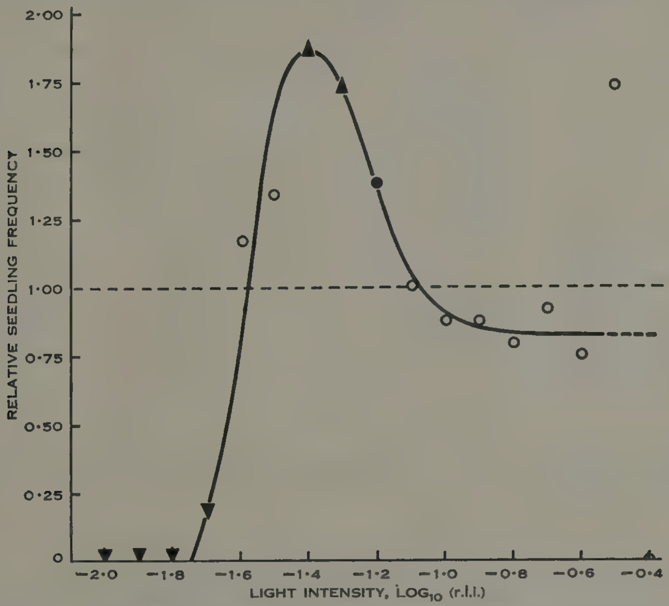

Fig. 7.—Relative frequency of *Phyllocladus* seedlings at various light intensity ranges. Data combined from quadrats IV, V, and VI. Each point gives the value of the ratio:

$$\frac{1}{K}\cdot\frac{\text{No. of seedlings}}{\text{No. of grid points}},\ \text{where}\ K=\frac{\text{total No. of seedlings}}{\text{total No. of grid points}},$$

for the light intensity range (plotted light intensity $\mp 0\cdot 10$). Significance of deviation of each ratio from the expected value ($1\cdot 0$) has been calculated by a χ^2-test; shown by: ○ $P>0\cdot 05$; ● $P<0\cdot 05$; ▼ $P<0\cdot 01$; ▲ $P<0\cdot 001$.

IV. DISCUSSION

The lower light intensity limit to seedling establishment was sharply defined for both species, and was probably set by the light intensity being too low to maintain a balance of photosynthesis over respiration. It can thus be considered as a naturally determined compensation point. The suddenness of the change from maximum to zero establishment (over the range 0·041 to 0·015 full daylight for kauri, and 0·042 to 0·018 for *Phyllocladus*) implies that seedling establishment was an "all or none" effect. The latter would be expected if the establishment was entirely light-determined at low intensities, but would be less likely if the compensation point was affected by seedling species interaction. It is therefore not likely that competition with other species greatly modified this field compensation point. The sharp definition of the limit also indicates that the germinating seedlings must all have had a similar response to low light intensities, despite the varied origin of the seed.

TABLE 3

VARIANCE OF DISTRIBUTION OF LOG$_{10}$ r.l.i. VALUES, AND SIGNIFICANCE OF DIFFERENCE OF VARIANCE, FOR ½-, 1½-, AND 2½-YEAR-OLD KAURI SEEDLINGS IN QUADRATS IV, V, AND VI

	Quadrat IV			Quadrat V			Quadrat VI		
	D.F.	Var. $\times 10^4$	Mean Log r.l.i.	D.F.	Var. $\times 10^4$	Mean Log r.l.i.	D.F.	Var. $\times 10^4$	Mean Log r.l.i.
½-yr-old kauri seedlings	7	17	−0·955	16	116	−1·088	6	557	−1·300
½- *v.* 1½-yr seedlings		1%*			1%			N.S.	
1½-yr-old kauri seedlings	37	114	−0·919	58	518	−1·129	63	448	−1·242
1½- *v.* 2½-yr seedlings		1%			N.S.			N.S.	
2½-yr-old kauri seedlings	20	307	−0·886	19	286	−1·138	20	474	−1·212
2½-yr seedlings *v.* grid		N.S.			1%			5%	
Quadrat grid points	48	263	−0·867	48	1113	−1·206	48	975	−1·334

*Significance of difference of variance values: N.S., not significant; 5%, significant at 5 per cent. level; 1%, significant at 1 per cent. level.

The well-defined high light intensity limit to kauri seedling establishment was unexpected and is not readily explained. It seems unlikely that the high light intensity as such would cause a complete inhibition of growth; yet the effect must have been due to some factor dependent on or associated with light intensity. For example, overhead cover, which affects light intensity at the forest floor, could have also affected seed distribution, and hence the establishment pattern obtained. Observations made showed that kauri seeds with their single wing and erratic flight in moving air were unlikely to be thus affected (cf. Mirams 1957); and although they did not always penetrate the undergrowth, where there were dense patches of the fern *Gleichenia circinata*, wind movement eventually allowed the seed to drop to the ground. Also, if the canopy had affected seed distribution, the maximum seed density would have been expected where the cover was least and light intensity highest. Alternatively the failure of kauri seedlings to establish at high light intensities may have been a consequence of solar heating of the soil, possibly through its hastening the drying out of the surface layers. Death of kauri seedlings in the field through desiccation has been noted (Mirams 1957). Greater wind movement in the less covered areas would contribute to this drying effect. This also provides a ready explanation of why no similar effect was observed for *Phyllocladus* seedlings. In the study area, soil heating and desiccation were most severe in early autumn (Mirams 1951), the period when the ephemeral kauri seed is shed and must germinate, before its short-term viability is lost. *Phyllocladus* seed was able to germinate at least partly in the spring, when the soil conditions are much more favourable: consequently, in the critical autumn period *Phyllocladus* seedlings had much better developed branch root systems. Thus a simple biological difference could have had considerable ecological consequences, affecting the relative ability of the two species to establish and survive.

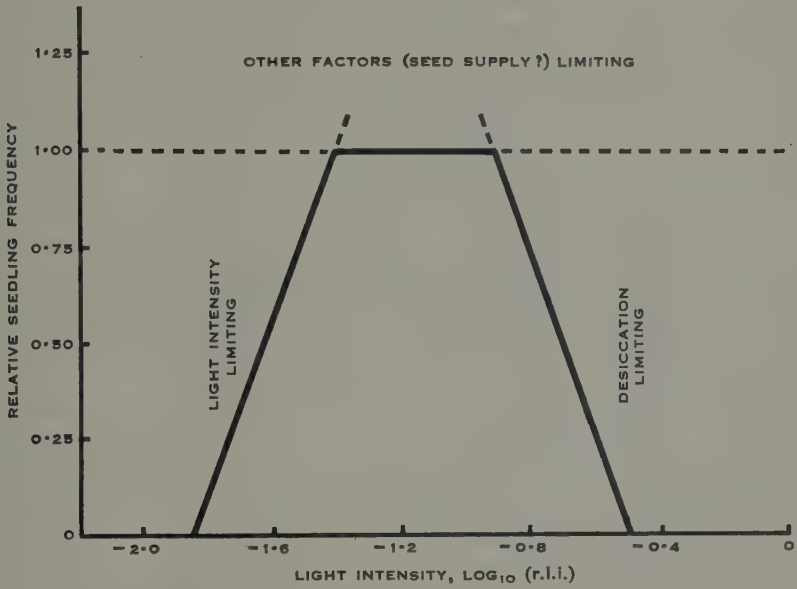
OTHER FACTORS (SEED SUPPLY ?) LIMITING
RELATIVE SEEDLING FREQUENCY
1·25
1·00
0·75
0·50
0·25
0
LIGHT INTENSITY LIMITING
DESICCATION LIMITING
−2·0
−1·6
−1·2
−0·8
−0·4
0
LIGHT INTENSITY, LOG10 (r.l.i.)

Fig. 8.—Diagrammatic representation of possible limits involved in the establishment of kauri seedlings.

The shape of the seedling establishment curve of kauri (Fig. 6) is therefore visualized as a random establishment pattern which has been limited at low intensities by an inadequate rate of photosynthesis, and at high intensities by soil heating and desiccation phenomena (Fig. 8). The reason for the *Phyllocladus* establishment curve showing a definite optimum at a low intensity (at 0·042 full daylight) is uncertain (Fig. 7). Possibly the moist dark conditions at the low light intensities were particularly favourable to seed germination and initial establishment, despite the low intensities limiting photosynthesis.

A comparison of Figures 1, 4, and 5 with Figures 6 and 7 shows that the optimum light intensity for establishment of both kauri and *Phyllocladus* seedlings in the ridge-top *Leptospermum* community studied was very close to the mode of the distribution of light intensities on the floor of that community. Furthermore, *Leptospermum* spp. are totally incapable of establishment under their own shade (only one dying seedling (of *L. ericoides*) was found in a careful examination of 300 m^2 of ground under semimature *Leptospermum*) and are consequently never seedling competitors. These two reasons seem adequate to explain the role of *Leptospermum* as a nursery crop.

These conclusions have been drawn from light measurements made in diffuse light only, though much of the light received by the seedling will have been direct sunlight from sunflecks. For comparative purposes (such as contrasting the behaviours of kauri and *Phyllocladus*) this does not matter, the two being subject to approximately the same errors. Nevertheless, the seedling distribution limits obtained are accurately set in terms of the method of measurement, and the question is one of what a light intensity measured in diffuse light means in terms of overall daylight conditions. The interdependence of diffuse light intensity and sunfleck frequency is such, at least for the *Leptospermum* community, that the values of the limits are unlikely to be out by more than a factor of 2. Such errors are less than the order of variation likely to be met from population to population of the same community, each with its own soil, water, temperature, and wind regime. The incomplete nature of the relationship between diffuse light and sunfleck frequency would become more important if the diffuse light measurements were used, as suggested in Section I, to compare the light regimes under two different communities. Some of the problems involved have been discussed by Evans (1956), who described an alternative method of measurement primarily concerned with the direct sunlight (sunfleck) component of the forest floor illumination. Which approach is used will depend on the type of vegetation being studied. Except in the extreme cases where one type of lighting greatly predominates, it would seem better to use both. Unfortunately, Evans's method would be hard to apply in a community such as the semimature *Leptospermum* studied here, where there is a dense ground flora; however, in such communities the diffuse light component is likely to be the more important one. The simple photographic method of light measurement advocated recently by Brown (1958) merits attention; the measurement obtained is essentially a "diffuse light" one.

Despite the assumptions involved, such approaches to the problem of studying light as an ecological factor can yield useful and reliable data. The conditions described here were exacting: the light pattern at the community floor was very broken, the two extremes of light intensity being found at points less than a metre apart; seedling frequencies were low (1–2/m^2); undergrowth was dense, making it difficult to move without damaging the vegetation—emphasizing that there may be physical limits to any method of measuring light intensities in a dense closed community. Despite these difficulties, this method may prove applicable to other similar autecological problems.

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FACTORS AFFECTING GROWTH AND DISTRIBUTION OF KAURI (*AGATHIS AUSTRALIS* SALISB.)

II. EFFECT OF LIGHT INTENSITY ON SEEDLING GROWTH

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Summary

The effect of various light intensities on the growth of kauri seedlings is described. Daylight was screened to the required level with lath screens. There was no significant effect of light on seedling mortality in the light intensity range 0·40–0·02 full daylight. Seedling morphology was affected by light intensity, the ratios stem dry weight/root dry weight, stem length/root length, and fresh weight/dry weight increasing significantly with decreasing light intensity. Seedling growth was a linear function of log (light intensity), the growth rates and assimilation rates being similar to those for other forest tree seedlings. The compensation point was at 0·009 full daylight, close to the low light intensity limit to seedling establishment in the field but low compared with those of other tree seedlings. There was no high light intensity limit to seedling growth, such as that shown for seedling establishment in the field. The apparent discrepancy is discussed.

I. INTRODUCTION

It has been shown (Bieleski 1959) that the distribution of young kauri seedlings in the field could be interpreted as one which was limited by both low and high light intensities. Most factors in the field do not vary without bringing about variation in some other factors, and it was suggested that the high intensities were taking effect, not through an effect of light *per se* but through heating effects and related soil drying induced by solar radiation. It was felt desirable to grow kauri seedlings at various light intensities under controlled conditions so that the light intensity could be varied, as far as possible, independently of other factors.

II. METHODS

(*a*) *Seed Planting*

Pure silica sand watered with mineral culture solution gave poor root growth and was unsuitable as a planting medium. A mixture of 4 parts volcanic soil (weathered basaltic scoria) to 1 of silica sand was found best. It was coherent, drained well, and supported good root growth, yet could be readily washed from the rootlets when seedlings were taken for measurement. It was occasionally watered with mineral culture solution (Long Ashton culture solution; Hewitt 1952) to ensure that there were no mineral deficiencies. Kauri is normally infected with an endotrophic mycorrhiza (Yeates 1924) and so the soil was inoculated with $\frac{1}{15}$

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of its volume of fresh litter, humus, and living root tissue from kauri forest. Care was taken to compact the soil evenly during boxing, since unduly heavy compacting was found to limit seedling growth slightly. Seed was supplied by the New Zealand Forest Service. Invariably some 80 per cent. of kauri seed is blind. Sound seed, identified by detecting the presence of the embryo and endosperm by lightly pressing the seed against the sorting table, was selected. The limited seed supply which was available came from two parent trees. The average weight of the sound seed from parent A was 0·033 g and from parent B 0·022 g; variation of seed weight within one type was very small. This difference made it desirable to keep the two seed types separate; though because of the low number of seeds available it was necessary to use both types in sowings. Seeds were sown 1 in. apart, two rows of type B seed alternating with one of type A, in boxes of 17 rows. The seed type of a given seedling could be recognized from its position in the box.

Seeds were planted wing uppermost to ensure maximum germination (Mirams 1951). A trial was sown to determine the best depth at which to plant seed. Three sets of 65 seeds were planted, the first with the base of the wing at the soil surface, the second with the base 1 cm beneath the surface, and the third with the base 2 cm beneath. Fifty-six of the surface-sown seeds (86 per cent.) germinated: only one (1·6 per cent.) germinated successfully at each of the other two depths, because many of the seeds had died under the soil after germinating as far as the radicle stage. The weak hypocotyl appeared unable to push the large winged seed through even a thin layer of soil. Thereafter, all seeds were sown at the soil surface.

The seed was germinated at 25°C, the optimum temperature for germination (Mirams 1951). After 2 weeks, when most of the viable seed had started to germinate, the boxes were shifted to the glass-house and left for a further 2 weeks till germination was complete. The boxes were then grouped into four pairs, each with the same number of germinated seedlings, and placed under the various treatments.

(*b*) *Light Screening*

Daylight was reduced to the required intensity by lath screens, which were used in preference to cloth or scrim screens for the following reasons. Lath screens can be directly constructed to give the exact degree of screening required; they do not fade and thus alter in their transmission factors; they hinder air movement less than cloth screens and thus have less effect on the humidity and temperature microenvironments; and they produce a heterogeneous light pattern of sunflecks and diffuse light which better approximates to field conditions.

Narrow cardboard strips soaked in paraffin wax were stapled onto a light wooden frame in the appropriate patterns to give screens with transmission factors of 0·500, 0·200, and 0·050. When these were checked by means of the photometric apparatus and the method employed in previous field studies (Bieleski 1959), the relative light intensity (r.l.i.) values measured under the screens were 0·481, 0·202, and 0·051 respectively; this showing that the light measurements made in the field could validly be compared with those of the glass-house experiments. The screens were used inside a glass-house and so allowance was made for the extra screening effect by photometrically measuring the (screen+glass-house) transmission factors (Table 1). The factors are referred to as 0·40, 0·20, 0·08, and 0·02 respectively.

The treatments covered the full range of light intensities met in the field. It was not practicable to place a fifth set outside the glass-house at full daylight intensity because of the very different temperature and moisture conditions, or to place all screens outside since the control of factors such as air movement and soil moisture would not have been adequate. In the glass-house, sunlight-induced soil temperature differences were kept minimal by maintaining the soil in a moist condition. The watering frequency varied from once every 1–2 days (0·40 light intensity, summer) to once every 12–20 days (0·02 light intensity, winter). Temperature differences were of a maximum order of 2–3°C, and an average of under 0·7°C. To avoid possible position effects the screen positions were changed weekly.

Table 1

SCREEN TRANSMISSION FACTORS IN THE GLASS-HOUSE

Screen	Transmission Factor
Glass-house alone	0·396 r.l.i.
Glass-house+0·50 screen	0·190 r.l.i.
Glass-house+0·20 screen	0·079 r.l.i.
Glass-house+0·05 screen	0·020 r.l.i.

(c) *Seedling Analysis*

Two samples were taken, one comprising one-third of the seedlings after 160 days of growth, and one the remaining two-thirds after 257 days of growth. Seedlings were carefully dug, numbered, and the seed type, box number, and position in the box (edge or non-edge) noted. The roots were dipped in water to loosen the soil and the remaining particles were brushed off with a camel's-hair brush. Seedlings were placed in a tray covered with a moist towel. A representative sample of five was selected and photographed. Ten criteria were used in analysing the seedling growth: total fresh weight, total dry weight, leaf dry weight, stem dry weight, root dry weight, number of leaves, number of stem branches, stem length, number of root branches, and root length. Each seedling was blotted dry with filter paper, weighed for total fresh weight, and separated carefully into leaves, stem, and roots. Measurements of leaf numbers, stem branch numbers, stem length, root branch numbers, and root length were made; then the pieces were dried at 100°C for 18 hr and 105°C for 6 hr, and equilibrated for 24 hr in a calcium chloride desiccator. The dry weights of leaf, stem, and roots were obtained and summed to give the total dry weight.

In making the measurements, the following arbitrary limits were fixed. The morphological division between stem and root was visible and definite, and was usually 1–1·5 cm below the soil surface. The two permanent cotyledonary leaves were regarded as true leaves, but young leaf primordia less than 2·5 mm long were not counted. Branch primordia less than 2 mm long were not counted as branches. In determining the stem length the length of the branches was included in the total with that of the main stem. Root branch number counts included all branches longer than 2 mm, though in assessing root length only those branches longer than 15 mm were included in the total.

(*d*) *Twin Leaf Analysis*

The twin leaf method of measurement of carbon assimilation has been quite widely used (see Portsmouth 1949). It depends on the measurement of the increase in dry weight of a set of leaves over a short assimilation period compared with a control set taken at zero time. Any increase is regarded as being entirely due to photosynthesized carbohydrates. There are inevitable errors due to translocation losses, and so the figures obtained are generally used to compare the effects of different treatments rather than as absolute measures of photosynthesis. If the two sets of leaves can be made up from twin leaves such as are found in many opposite-leaved species, the sampling error is considerably less. In the seedling stage kauri has opposite twin leaves. The variation in dry weight between individuals of a pair was slight, the standard error of the mean being ±0·9 per cent. for samples of 50.

The seedlings were grown under four light intensities as already described. The experiment was carried out on an "average" day, with sunlight broken by light clouds, so that the results were comparable with those from other experiments. At dawn one leaf of each chosen pair was excised with a sharp scalpel and put in a moist petri dish. Where several pairs were taken from the one stem, the zero-time leaves were taken from both sides of the stem. Photographic prints of the leaves were made and the total area of each set estimated planimetrically. The leaves were dried at 100°C for 18 hr and 105°C for 6 hr, then equilibrated for 24 hr in a calcium chloride desiccator before weighing. At sunset the paired sets were similarly collected, printed, and weighed.

III. Results

(*a*) *Non-Treatment Variation*

Analyses of variance were made to determine whether there were any non-treatment variations. It was found that all treatments showed the same features: there were no significant differences between boxes of a treatment or positions within a box, but seedlings from the two seed types were significantly different. It was therefore necessary to keep data from the two seed types separate, though treatment data for the two boxes and the different positions within the box could be combined.

(*b*) *Seedling Mortality*

The germination rate and seedling mortality of seedlings from the two seed types were significantly different (Table 2). No significant effect of light intensity on seedling mortality could be shown for either seed type. It was legitimate to combine the mortality data since the two seed types were present in all treatments in the same proportion. The differences in mortality rate between treatments were still not significant (Table 3).

TABLE 2

EFFECT OF SEED TYPE ON SEED GERMINATION AND SEEDLING MORTALITY*

Seed Type	Seeds Planted	Seeds Germinated	Percentage Germination	Survivors after 3 Months	Seedling Mortality	Percentage Mortality
A	936	481	51·3	424	57	11·9
B	1716	478	27·8	375	103	21·6
Total	2652	959	36·2	799	160	16·7

χ^2 for difference in germination rate = 92·8, in mortality rate = 13·4: for both differences, $P<0\cdot001$

* Includes data from treatments other than those reported in this paper.

(c) *Seedling Analyses*

Means of the individual character measurements made after 160 days (sample I) and 257 days (sample II) are presented in Table 4. When total dry weight was taken as the best index of plant growth, the differences between treatments were shown to be significant (Table 5). It can be seen that the two seed types had a

TABLE 3

MORTALITY OF SEEDLINGS UNDER DIFFERENT LIGHT INTENSITIES

Relative Light Intensity	Seeds Germinated	Survivors after 3 Months	Seedling Mortality	Percentage Mortality
0·40	121	107	14	11·6
0·20	123	108	15	12·2
0·08	127	104	23	18·1
0·02	128	107	21	16·4
Total	499	426	73	14·6

χ^2 for difference in mortalities = 2·59 (3 degrees of freedom): difference not significant ($P>0\cdot1$)

TABLE 4

EFFECT OF LIGHT INTENSITY ON GROWTH OF KAURI SEEDLINGS

Sample	Light Intensity	No. of Seedlings	Fresh Weight (mg)	Dry Weight (mg)				No. of Leaves	No. of Stem Branches	Mean Stem Length (cm)	No. of Root Branches	Mean Root Length (cm)
				Total	Leaf	Stem	Root					
IA	0·40	16	256	56·5	24·4	20·0	12·2	6·4	1·2	6·6	7·0	8·1
	0·20	23	240	49·6	21·8	16·9	10·9	5·4	1·2	5·9	6·7	6·5
	0·08	27	172	31·0	13·1	11·0	7·0	4·3	0·8	5·1	3·8	4·1
	0·02	16	141	25·0	10·0	10·1	4·8	2·0	0	4·9	2·1	3·1
IB	0·40	21	181	40·2	17·8	14·2	8·1	5·4	0·8	4·8	3·4	5·9
	0·20	14	160	30·7	13·3	10·9	6·5	4·4	0·8	4·4	3·1	4·7
	0·08	10	116	19·9	8·4	7·5	4·0	3·7	0·4	3·9	1·7	2·6
	0·02	21	90	14·9	5·9	6·5	2·5	2·0	0	3·6	0·5	1·9
IIA	0·40	37	679	190·0	81·9	58·6	49·5	13·8	3·7	10·1	24·3	22·4
	0·20	37	572	145·4	66·3	48·1	31·0	12·4	3·6	10·2	18·0	19·6
	0·08	39	318	75·7	35·6	25·5	14·7	8·3	2·4	7·5	6·9	9·5
	0·02	37	180	33·4	14·3	12·3	6·8	4·2	0·8	5·7	2·6	4·4
IIB	0·40	33	457	122·5	53·3	40·0	29·2	11·6	2·5	7·8	13·6	15·6
	0·20	34	326	80·5	36·8	27·2	16·6	10·1	2·9	7·2	7·5	9·8
	0·08	28	163	34·3	15·0	12·8	6·6	5·4	1·4	4·9	2·6	4·4
	0·02	33	115	19·5	7·8	7·7	3·9	2·9	0·4	4·0	0·6	2·2

common pattern of behaviour (Table 4). The most definite trend was towards a poorer root development and better leaf and stem development, relative to the total dry weight, with decrease in light intensity. There was also a tendency for the fresh weight/dry weight ratio to increase at low light intensities. By calculating the individual ratios for each seedling in the various sets, these trends were shown to be statistically significant (Table 5). They were partly a function of the treatment itself, but also partly a function of the different seedling sizes which were present under the different treatments. Thus when similar-sized seedlings were selected from the range of sizes present in two treatment groups and compared, the differences in seedling morphology between treatments were smaller.

TABLE 5

SIGNIFICANCE OF DIFFERENCE OF SEEDLING DRY WEIGHT AND SEEDLING DEVELOPMENT RATIOS IN SEEDLINGS GROWN AT VARIOUS LIGHT INTENSITIES

Sample I taken after 160 days' growth, sample II after 257 days' growth

Character	Sample and Seed	Mean 0·40 r.l.i.	0·40 *v.* 0·20	Mean 0·20 r.l.i.	0·20 *v.* 0·08	Mean 0·08 r.l.i.	0·08 *v.* 0·02	Mean 0·02 r.l.i.
Total dry wt. (g)	IA	0·0565	5%*	0·0495	1%	0·0310	5%	0·0249
	IB	0·0402	5%	0·0307	5%	0·0199	5%	0·0149
	IIA	0·1900	1%	0·1454	1%	0·0757	1%	0·0334
	IIB	0·1225	1%	0·0805	1%	0·0342	1%	0·0195
Ratio of stem dry wt. to root dry wt.	IIA	1·23	1%	1·58	1%	1·91	N.S.	1·89
	IIB	1·47	1%	1·76	1%	2·17	N.S.	2·21
Ratio of stem length to root length	IIA	0·51	N.S.	0·56	1%	0·90	1%	1·41
	IIB	0·57	1%	0·81	1%	1·41	5%	2·16
Ratio of fresh wt. to dry wt.	IIA	3·59	1%	3·95	1%	4·28	1%	5·41
	IIB	3·76	1%	4·12	1%	4·87	1%	6·07

* Significance of difference of two means: N.S., not significant; 5%, significant at 5 per cent. level ($P < 0{\cdot}05$); 1%, significant at 1 per cent. level ($P < 0{\cdot}01$).

To some extent the measurements of growth were all biased by the original seed, most noticeably at the lowest light intensities where the seedling growth was the slowest. For example, a seedling living at the compensation point would show no net growth yet would possess from the time of germination stem, root, and leaves. To eliminate this error the growth increments over the 97 day period between sample I and sample II can be examined. The trend towards an increase in shoot development at the expense of the roots is even more pronounced.

(*d*) *Twin Leaf Assimilation Experiments*

Results obtained for the assimilation period 6 a.m. to 6 p.m. are given in Table 6.

IV. DISCUSSION

The increase in the shoot/root ratio at low light intensities has been noted for other species, both in the field (Aldrich-Blake 1932; Harley 1939; Coile 1940; Kozlowski 1949) and under controlled conditions of growth (Mitchell 1936; Barney 1951); and appears to be bound up with nitrogen metabolism (Mitchell 1954).

TABLE 6

DRY WEIGHT INCREMENTS IN LEAVES DURING 12 HOURS' ASSIMILATION AT VARIOUS LIGHT INTENSITIES

Treatment	No. of Twins	Leaf Area of Sample (cm^2)	Dry Wt., Sample I (g)	Dry Wt., Sample II (g)	Increment (g/g dry wt.)	Increment (g/dm^2)
0·40 r.l.i.	71	38·0	0·2715	0·2889	0·064	0·045
0·20 r.l.i.	64	43·7	0·2818	0·2915	0·034	0·022
0·08 r.l.i.	45	28·0	0·1691	0·1724	0·019	0·011
0·02 r.l.i.	33	20·9	0·1348	0·1346	−0·001	−0·001

From the total dry weight increments over the 97 days from sample I to sample II, the growth rates have been calculated (Table 7) by means of the growth rate formula of Blackman (1919):

$$r = (1/t) \log_e W_2/W_1,$$

where r is the geometric growth rate; t the number of days from sample I to sample II; W_1 the mean dry weight of sample I; and W_2 the mean dry weight of sample II. When the two seed types are compared (Table 7), the growth rates are found to be very similar despite the large differences in the seedling dry weights. When growth rates were calculated for the 257 day period from the time of planting to sample II, the seed dry weight being used as W_1, the similarity was more marked, as the difference was less than 20 per cent. in all cases. Thus the original difference in the seed weight, and not any difference in growth rate, was responsible for the

TABLE 7

SEEDLING GROWTH RATE AT DIFFERENT LIGHT INTENSITIES

Light Intensity	Seedling Growth Rate (g/g/day)		
	Seed Type A	Seed Type B	Mean
0·40 r.l.i.	0·0125	0·0115	0·0120
0·20 r.l.i.	0·0110	0·0099	0·0104
0·08 r.l.i.	0·0091	0·0057	0·0074
0·02 r.l.i.	0·0029	0·0027	0·0028

marked differences in seedling dry weights. This illustrates Blackman's (1919) statement that "other things being equal a small seed is a permanent handicap to the plant".

At the higher light intensities (but not the lower ones) these rates of growth are slow compared with those of such herbaceous plants as *Helianthus annuus* (0·100 g/g/day at 0·40 r.l.i.), *Trifolium subterraneum* (0·090 g/g/day at 0·40 r.l.i.), and *Geum urbanum* (0·060 g/g/day) (Blackman and Wilson 1951*a*); but are typical of rates for forest tree seedlings—for example, *Sequoia sempervirens* (0·006–0·012 g/g/day at 0·40 r.l.i.) and *Pinus taeda* (0·015–0·025 g/g/day) (Shirley 1929).

An approximate value for the assimilation rate of individual leaves can be obtained, since in the twin leaf experiments the apparent assimilation rate measured is likely to be about two-thirds of the true assimilation rate (40 per cent. of the assimilate utilized in leaf growth, since (leaf dry weight)/(total dry weight) = 0·40–0·44; and approximately half the remainder translocated during the half-day). If carbohydrate formation be assumed, the assimilation rates are therefore approximately equivalent to 8·0, 4·0, and 2·0 mg carbon dioxide assimilated per sq. decimetre per hour at 0·40, 0·20, and 0·08 r.l.i. respectively. These values are close to those obtained for individual *Pinus taeda* needles and for *Quercus alba* and *Q. borealis* seedling leaves (Kramer and Decker 1944; Kramer and Clarke 1947), and intermediate between those for shade herbs (*Oxalis*, *Philodendron*) and sun annuals (*Helianthus*, *Nicotiana*) (Bohning and Burnside 1956). Kauri behaviour, therefore, is similar to that of normal shade-tolerant seedlings and plants.

The twin leaf data indicate that the compensation point for kauri seedlings at normal temperatures is in the region of 0·02 r.l.i. The average growth rate values quoted in Table 7 can be used to derive a more accurate figure for this compensation point (Fig. 1). This was found to be at an intensity of 0·009 r.l.i. for seedlings grown under glass-house conditions. It is similar to the lower light intensity limit (0·015 r.l.i.) for seedling establishment in the field (Bieleski 1959), which confirms the suggestion made that the establishment limit in the field was set by low light intensities limiting photosynthesis. The closeness of the correspondence, particularly when allowance is made for the optimal soil conditions in the glass-house experiments, indicates that it is the sole factor involved.

This compensation point can be compared with those reported for other species. Bates and Roeser (1928) for various *Pinus* spp. give values which, on the basis of measurement used here, fall in the range 0·04–0·10 r.l.i. Their values for *Pseudotsuga taxifolia* (0·03 r.l.i.), *Pinus ponderosa* (0·02 r.l.i.), and *Sequoia sempervirens* (0·015 r.l.i.) compare well with those of Baker (1945), who quotes 0·03 r.l.i., 0·005–0·015 r.l.i., and 0·02–0·03 r.l.i. respectively. Shirley (1929) gives data which indicate compensation points for *Sequoia* and *Pinus taeda* in the range 0·01–0·02 r.l.i. For a number of herbaceous plants, Blackman and Wilson (1951*a*, 1951*b*) found compensation points in the range 0·07–0·18 r.l.i., and concluded that the values of the compensation point do not differ widely between species, and that the ability of different species to withstand shading cannot be attributed to major variations in the compensation point. It can be seen from the figures for forest tree seedlings quoted above that whilst these statements may apply to certain groups of herbaceous plants, they are incorrect as generalizations. Some differences can of course be explained by the widely differing methods used. However, the compensation point for kauri, obtained by three distinct methods including one very similar to that of Blackman and Wilson, is eight times as low as the lowest compensation point they quote (0·07 r.l.i.). As an illustration, over 95 per cent. of the kauri seedlings which establish in *Leptospermum* shrubland (Bieleski 1959) do so at light intensities below the compensation point of *Hordeum vulgare* (Blackman and Wilson 1951*a*). The values for the compensation point differ widely for different species, though for forest tree seedlings many seem to fall in the range 0·005–0·070 r.l.i. The compensation point for kauri falls at the lower end of this range. The statement of Cockayne (1928) that "*Agathis* is strongly light-demanding" cannot be regarded as correct, at least for the seedling; and his view that kauri is replaced by *Beilschmiedia* spp. because kauri seedlings are unable to tolerate low light intensities is in need of re-examination. They will survive at intensities as low as 0·02 r.l.i., though recognizably etiolated, yet will grow rapidly once any breach in the cover occurs (Sando 1936).

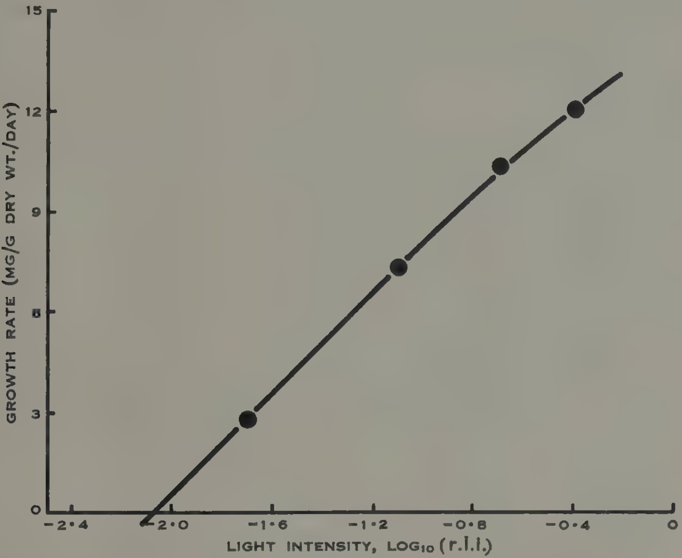

Fig. 1.—The linear relationship of seedling growth rate to log (light intensity), used to estimate the compensation point. The extrapolated growth rate/light intensity line indicates a compensation point at the light intensity $\log_{10}$ (r.l.i.) = −2·18, that is, r.l.i. = 0·009.

In glass-house experiments there was no decrease of photosynthesis at high light intensities (Table 6, Fig. 1); nor does light have any effect on the germination rate (Mirams 1951) or on seedling mortality. In the field, however, kauri did not establish under *Leptospermum* at light intensities higher than 0·30 r.l.i. (Bieleski 1959). The glass-house experiments show that this could not have been due to any direct effect of the light itself, even though the responsible factor must have been dependent on light in some way. In addition it must have been one which operated in the field, but not in the glass-house experiments. The only factors which seem to fulfil these requirements are those of seed distribution (discounted as a possibility; Bieleski 1959), soil temperature, and soil moisture.

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FACTORS AFFECTING GROWTH AND DISTRIBUTION OF KAURI (*AGATHIS AUSTRALIS* SALISB.)

III. EFFECT OF TEMPERATURE AND SOIL CONDITIONS

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Summary

Kauri (*Agathis australis*) seedlings were grown under controlled conditions of temperature, soil moisture, and exposure to mycorrhizal infection. High temperatures inhibited root growth; seedlings exhibited a growth optimum at 23–26°C; the evidence suggested that both trees and seedlings were dormant when the maximum temperature fell below 17°C. Seedlings were generally resistant to both waterlogging and drought: waterlogging caused a decrease in root length and branching, but did not affect the root weight; drought increased root development at the expense of the stems. In the field, seedlings were liable to be killed by drought in the first few months of growth. The "high light intensity limit" to seedling establishment previously observed in the field was apparently caused by greater solar radiation increasing soil desiccation during this critical period. Seedlings grown in sterile soil and those exposed to mycorrhizal infection showed no significant differences.

The autecology of kauri is discussed in the light of current knowledge. The altitudinal and latitudinal limits could be caused by temperature limiting the rate of growth and also the length of the growing season. Kauri appears to occur preferentially on ridge-top sites because of its tolerance of poor soils and its resistance, once established, to drought. The inability of kauri seedlings to establish under cover of the mature tree is thought to be caused by root competition effects. Kauri is no longer regarded as a seral stage in the development of a hardwood climax, but as one component of a "regeneration complex".

I. Introduction

An investigation into the effects of light on the growth and establishment of kauri seedlings has revealed that, while light intensity was one factor affecting kauri seedling establishment, other factors were also involved (Bieleski 1959*a*, 1959*b*). Evidence suggested that soil temperature and soil moisture were likely to be important. Glass-house experiments were therefore conducted and field observations made in order to study the effects of temperature, soil moisture, soil mycorrhiza, and soil type on the growth of kauri.

II. Methods

(*a*) *Seed Planting*

Seeds for the temperature and soil mycorrhiza experiments were from two parent trees, A and B, drawn from the same stock as used in the previous light intensity experiments. They were sown and germinated in the same way (Bieleski

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1959*b*), except that in the soil mycorrhiza experiments the soil was sterilized. Seeds for the soil moisture experiments were type C, from a third parent tree, and were sown in the standard soil mixture 2·5 cm apart, in large deep unglazed earthenware pots.

(*b*) *Seedling Analysis*

Seedlings grown under the various treatments were analysed by means of the same methods and measurements as for the light intensity experiments (Bieleski 1959*b*).

(*c*) *Temperature Control*

Without a large refrigerating unit it is difficult both to grow seedlings at temperatures below that of air, and to maintain them at any controlled temperature when the seedlings are grown in sunlight. Evidence suggested that in Auckland temperatures were suboptimal for kauri growth, and therefore it was felt that useful information would still be obtained when only temperatures at or above air temperature were used. Three longitudinal halves of 44-gal oil drums held on wooden supports were fitted at the top with wooden frames which supported covering sheets of glass. Small gaps were left at each end to allow adequate gas exchange. Water in the bottom of two of the tanks was kept at the required temperature by a heater, thermostat, and stirrer. Tap-water ran continuously through the third. In all, the water temperature fully controlled the temperature of the air above. The seed boxes were supported above the surface of the water. To avoid complications through the heating effects of direct sunlight, the baths were placed in a small building-well, never lit by direct sunlight but open to the south so that about a third of the sky hemisphere still lit the area. The average light intensity was measured and found to be about 20 per cent. full daylight (0·20 relative light intensity (r.l.i.)) and thus typical of field intensities, though the light was much more blue than usual (colour temperature of blue sky 25000°K, of overcast sky 7000°K, and of direct sunlight 6000°K; Cooper and Probine 1954; Hull 1954). Lighting conditions were therefore somewhat artificial. Tank positions were interchanged once a month to minimize position effects. Sample I, of one-third of the total number of seedlings, was taken after 163 days, and sample II, of the remaining two-thirds, after 235 days. Measurements of assimilation rate were also made, by means of the twin leaf method employed in similar measurements at different light intensities (Bieleski 1959*b*).

(*d*) *Soil Water Conditions*

It was decided that for a long-term experiment the most satisfactory method of providing definite conditions of soil moisture was to keep the water-table in the soil at a constant level. To do so, the pots containing the soil and seeds were placed inside slightly larger pots with plugged drain holes. A hole was bored in the outer pot at the required level, and a slow flow of water through a capillary into the outer pot maintained the water level. All pots were placed in the glass-house under the maximum available light intensity (0·40 r.l.i.). Four watering conditions were used: "waterlogged", with water at the soil surface; "semi-waterlogged", with the water level 2 cm below the soil surface; "normal", with the water level 10 cm below the soil surface; and "dry". The last treatment could not be obtained by any practicable water-table method, since a soil column of about 70 cm would have been required. The pot was therefore watered lightly and regularly in amounts such that the soil was never more than slightly moist at the surface and normally powder-dry. In later stages a small plant of *Taraxacum*, less drought resistant than kauri, served by its wilting symptoms as a useful indicator. The soil moisture was therefore kept for a large fraction of the time not much above wilting point for this herb. One sample was taken, after 302 days.

(*e*) *Soil Mycorrhiza*

After inoculation with kauri soil, litter, and root tissue, the standard soil mixture was sterilized by low pressure steaming for 25 min, as recommended by Lawrence and Newell (1942). The seeds were dusted with "T.M.T.D." fungicide, and in the case of the sterile treatment, planted directly into the soil. For the control, the sterilized soil was first reinoculated with fresh kauri soil and root material, then the seeds were planted. This inoculation was repeated 3 weeks later. Boiled water was used throughout for watering, and boxes were held at full glass-house illumination (0·40 r.l.i.).

Table 1

MORTALITY OF SEEDLINGS GROWN AT DIFFERENT TEMPERATURES

Temperature	Seeds Germinated		Survivors after 3 Months		Seedling Mortality		Percentage Mortality
20°C	64	128	57	112	7	16	10·9
	64		55		9		14·1
25°C	57	121	47	99	10	22	17·5
	64		52		12		18·8
30°C	69	122	50	83	19	39	27·6
	53		33		20		37·8
Total		371		294		77	20·7

χ^2 for differences in mortality = 12·0 (2 degrees of freedom); $P<0\cdot01$

III. Results

(*a*) *Temperature*

Over the course of the experiment the tap-water temperature rose from 17 to 22°C, and the temperatures in the other two baths were raised from 22 to 27°C and from 27 to 32°C. The average temperatures were 20, 25, and 30°C respectively.

(i) *Mortality*.—Seedling mortality was significantly higher at higher temperatures (Table 1).

(ii) *Dormancy.*—Previous trials had shown that under some conditions germinating kauri seedlings would develop as far as the cotyledonary stage and then show no further growth. This dormancy was sometimes maintained for over 3 months. Evidence which suggested that this may have been primarily a temperature effect was obtained when counts were made of the numbers of seedlings which had passed the cotyledonary stage after a given time at the various temperatures. The seedlings were germinated during 7 days at 25°C, then hardened off in the glass-house at an average temperature of 16°C for 3 weeks. During this time all seedlings remained at the cotyledonary stage, showing no apical growth from the embryonic bud. Seedlings were then placed under the various treatments, and after 22 days a count was made of the number of seedlings which had broken dormancy and put out a small shoot (Table 2). The number was significantly higher at 22 and 27°C than at 17°C.

TABLE 2

EFFECT OF TEMPERATURE ON SEEDLING DORMANCY

Temperature	No. of Seedlings		No. Breaking Dormancy		Percentage Breaking Dormancy
17°C	61	124	2	7	3·3
	63		5		7·9
22°C	53	114	16	37	30·2
	61		21		34·4
27°C	47	113	12	41	25·6
	66		29		44·0

χ^2 for differences in numbers breaking dormancy = 27·6 (2 degrees of freedom); $P<0{\cdot}001$

(iii) *Seedling Analyses.*—An analysis of variance on the collected data showed that there were no box or edge effects, but that there were significant differences in the seedlings from the two seed types. Means of the individual character measurements for sample II of both seed types are presented (Table 3). It was found on analysis that at the time of sample I insufficient growth had occurred for significant differences to develop between treatments, and so the results have not been included.

When total dry weight was taken as the best index of growth, the differences between treatments were shown to be significant for type A seedlings but not for type B (Table 4). Relative to the total dry weight, root development was poorer and stem development better at higher temperatures in both seedling types. By calculating the individual ratios for each seedling these trends were shown to be significant (Table 4).

There were also visible differences in root development. At the highest temperature the roots had a darker, more suberized appearance, and lacked the normal

TABLE 3

EFFECT OF TEMPERATURE, SOIL MOISTURE, AND SOIL MYCORRHIZA ON KAURI SEEDLING GROWTH

Treatment	No. of Seedlings	Fresh Weight (mg)	Dry Weight (mg)				No. of Leaves	No. of Stem Branches	Stem Length (cm)	No. of Root Branches	Root Length (cm)
			Total	Leaf	Stem	Root					
Seed A, 20°	47	400	92·0	40·5	30·9	20·6	8·0	2·4	8·2	11·8	14·8
25°	31	522	122·8	55·8	42·1	24·9	11·7	3·7	10·8	16·1	16·3
30°	34	313	75·3	34·1	26·8	14·4	9·9	2·9	7·7	6·2	8·8
Seed B, 20°	29	313	70·1	29·9	23·1	17·1	7·3	2·0	6·6	9·7	12·7
25°	34	320	71·8	33·6	23·3	15·0	9·5	2·9	7·3	7·7	9·8
30°	21	255	60·8	27·7	21·4	11·5	8·8	2·5	7·0	5·0	7·8
Waterlogged	43	549	173·4	76·4	67·3	29·7	15·7	3·5	11·7	3·9*	11·9
Semi-waterlogged	52	573	170·3	78·7	63·1	28·5	14·4	3·5	11·2	3·7*	11·5
Normal	54	698	201·8	90·7	77·9	33·2	19·4	4·0	14·3	5·8*	17·3
Dry	53	679	188·9	88·5	58·7	41·7	18·7	3·5	13·3	9·5*	37·5
Seed A, control	37	290	66·0	29·9	21·5	14·6	7·2	1·6	6·3	6·9	10·1
Seed A, sterile	28	312	69·4	33·8	22·5	13·1	7·9	1·5	7·0	6·9	9·5
Seed B, control	24	184	39·8	19·0	12·7	8·1	5·5	0·8	4·8	3·4	6·4
Seed B, sterile	23	185	35·4	15·5	13·0	6·9	5·6	0·8	4·8	2·4	6·1

*Only branch roots longer than 15 mm counted.

white growing apices. A slight apparent decrease in water content with increase in temperature was not significant.

Information from the experiments was not adequate enough to permit of deriving an accurate optimum temperature for the growth of kauri seedlings, although the region 23–26°C was indicated. The difference in behaviour of the two seed types indicates that it is unlikely that any well-defined optimum exists.

TABLE 4

SIGNIFICANCE OF DIFFERENCE OF SEEDLING DRY WEIGHT AND SEEDLING DEVELOPMENT RATIOS IN SEEDLINGS GROWN AT VARIOUS TEMPERATURES

Character	Seed Type	Mean, 20°C	20° *v.* 25°	Mean, 25°C	25° *v.* 30°	Mean, 30°C
Total dry wt. (g)	A	0·0920	1%*	0·1228	1%	0·0753
	B	0·0701	N.S.	0·0718	N.S.	0·0608
Ratio of stem dry wt. to root dry wt.	A	1·57	5%	1·78	5%	2·08
	B	1·50	N.S.	1·70	5%	2·07
Ratio of stem length to root length	A	0·61	1%	0·74	1%	1·04
	B	0·65	5%	0·92	5%	1·29
Ratio of wet wt. to dry wt.	A	4·37	N.S.	4·29	N.S.	4·26
	B	4·53	N.S.	4·56	N.S.	4·47

* Significance of difference of two means: N.S., not significant; 5%, significant at 5 per cent. level ($P<0\cdot05$); 1%, significant at 1 per cent. level ($P<0\cdot01$).

(iv) *Assimilation Rates by the Twin Method.*—Results obtained for a 12-hr assimilation period were as follows (Table 5). The assimilation rate was highest at the highest temperature.

TABLE 5

DRY WEIGHT INCREMENTS IN LEAVES DURING 12 HOURS' ASSIMILATION AT VARIOUS TEMPERATURES

Temperature	No. of Twins	Leaf Area of Sample (cm^2)	Dry Wt., Sample I (g)	Dry Wt., Sample II (g)	Increment (g/g dry wt.)	Increment (g/dm^2)
21°C	49	29·4	0·2290	0·2334	0·019	0·015
26°C	59	32·4	0·2049	0·2111	0·030	0·019
31°C	49	29·7	0·2033	0·2113	0·039	0·027

(b) *Soil Moisture*

(i) *Mortality.*—There were no significant differences in mortality under the different treatments (Table 6).

(ii) *Seedling Analyses.*—The results are presented in Table 3. With the use of total dry weight as the best index of growth, it was shown that seedlings grown under normal conditions of watering grew better than under either of the extremes (Table 7). It can be seen that the semi-waterlogged and waterlogged treatments had an identical effect. Root development (but not root dry weight) was adversely affected by waterlogging and stimulated by dry conditions. Except in the dry treatment, where the stem weight was somewhat lowered at the expense of root development, there was little effect of the treatments on stem development. There was also a trend for the "succulence" (fresh wt./dry wt.) of the seedlings to increase with soil dryness. By calculating the individual ratios for each seedling, these trends were shown to be significant (Table 7).

TABLE 6

MORTALITY OF SEEDLINGS GROWN UNDER DIFFERENT SOIL MOISTURE CONDITIONS

Soil Moisture	Seeds Germinated	Survivors after 6 Months	Seedling Mortality	Percentage Mortality
Dry	56	53	3	4·6
Normal	55	54	1	1·5
Semi-waterlogged	55	52	3	4·6
Waterlogged	49	43	6	9·2
Total	215	202	13	6·0

χ^2 for differences in mortality = 5·1 (3 degrees of freedom); not significant

TABLE 7

SIGNIFICANCE OF DIFFERENCE OF SEEDLING DRY WEIGHT AND SEEDLING DEVELOPMENT RATIOS IN SEEDLINGS GROWN UNDER VARIOUS SOIL MOISTURE CONDITIONS

Semi, semi-waterlogged; WL, waterlogged

Character	Mean, Dry	Dry *v.* Normal	Mean, Normal	Normal *v.* Semi	Mean, Semi	Semi *v.* WL	Mean, WL
Total dry wt. (g)	0·1889	N.S.*	0·2018	5%	0·1703	N.S.	0·1734
Stem dry wt. (g)	0·0587	1%	0·0779	5%	0·0631	N.S.	0·0673
Root dry wt. (g)	0·0417	1%	0·0332	N.S.	0·0285	N.S.	0·0297
Root branches (No.)	9·96	1%	5·79	1%	3·73	N.S.	3·93
Ratio of stem wt. to root dry wt.	1·40	1%	2·36	N.S.	2·30	N.S.	2·30
Ratio of stem length to root length	0·39	1%	0·92	5%	1·06	N.S.	1·03
Ratio of fresh wt. to dry wt.	3·65	1%	3·54	1%	3·39	1%	3·20

* Significance of difference of two means: N.S., not significant; 5%, significant at 5 per cent. level ($P<0·05$); 1%, significant at 1 per cent. level ($P<0·01$).

Seedlings from both waterlogged and semi-waterlogged treatments had hypertrophied lenticels, 1–2 mm long, on the basal part of the stem just below the soil surface. The roots were also covered with a weft of fungal hyphae which had some of the characteristics of an ectotrophic mycorrhiza. These were not seen in any other treatment or in nature. The normal mycorrhiza in kauri is the endotrophic nodule-forming type. The roots were also a darker brown than usual, though still showing white growing tips (as noted for flooded *Pinus* spp.; Hunt 1951).

(c) *Soil Mycorrhiza*

(i) *Seed Germination and Mortality.*—Germination was significantly better in sterile soil (Table 8). Because of an accident, the data on seedling mortality are incomplete, though it is known that the mortality rate was considerably higher in the sterile boxes (more than 40, compared with less than 15).

TABLE 8

EFFECT OF SOIL STERILITY ON SEED GERMINATION

Treatment	Seeds Planted		Seeds Germinated		Percentage Germination
Sterile	204	408	106	206	52·0
	204		100		49·0
Non-sterile	204	408	62	127	30·4
	204		65		31·8
Total	816		333		40·8

χ^2 for differences in germination = 18·7 (1 degree of freedom); $P<0{\cdot}001$

(ii) *Seedling Analyses.*—Means of the individual character measurements are presented in Table 3. There were only slight and non-significant differences between treatments. Mycorrhizal infection may not have occurred, as mycorrhizal nodules were not observed in any plants from either treatment.

IV. DISCUSSION

(a) *Temperature*

The temperature experiments were of necessity carried out under conditions of high humidity, which would have favoured fungal growth. The increased mortality at higher temperatures was therefore probably due to the more ready growth of damping-off fungi, which were the main cause of seedling death.

Some of the temperature effects on the morphology of kauri seedlings have been noted for other plants. The development of a suberized appearance in the roots at high temperatures was observed in *Pinus taeda* at 35°C (Barney 1951) and *Lolium perenne* at 32°C (Mitchell 1954); in each case, as with kauri, it was associated with a decrease in root growth.

The twin leaf experiments show that carbon dioxide assimilation probably had a higher temperature optimum than seedling growth. This suggests that the optimum for growth was not set by high temperatures limiting photosynthesis but through their causing a disproportionate increase in the respiration losses. The growth temperature optimum obtained (23–26°C) was higher than that of a species adapted for growth in temperate regions, though lower than that of truly tropical species (its ecological characteristics are also those of a subtropical species; Robbins 1957). However, growth temperature optima are known to be dependent on various factors, for example, light intensity (Went 1945).

The most significant temperature effect was on the breaking of bud and seedling dormancy—very slow at 17°C but rapid at temperatures above 20°C. The phenomenon was shown in other experiments. Seedlings grown in a growth chamber for 10- and 16-hr day lengths showed no breaking over 3 months at 16°C, yet broke rapidly in both sets when the temperature was raised to 19°C. A similar set of seedlings sown in the glass-house remained dormant during winter and started growth in August (earlier than in the field), when the average glass-house temperature was only 15–16°C but the daily maximum often reached 19°C. Field records indicate that mature trees may show the same phenomenon. It was found that in the Waitakere Ranges, kauri was dormant during the winter and formed resting buds, the spell lasting from late April until late August or September. Temperature data for kauri forest in this area (Mirams 1951) show that the period of dormancy corresponds exactly with the period during which the weekly maximum temperature lies below 17·5°C. The evidence, although incomplete, strongly suggests that there is a limiting maximum temperature of 17°C below which kauri does not grow (cf. sugar-cane; Das 1933). It is still possible that the mean or minimum temperature may be important, or that photoperiodic effects are also involved (Olson and Nienstaedt 1957). It would be desirable for more work to be carried out on this problem.

One suggestion for the latitudinal and altitudinal limits, at 38° S. and 600 m, to kauri distribution, is that kauri is killed by frost. This has been shown to be the case for the mangrove, *Avicennia officinalis*, which has the same southern limit as kauri (Chapman and Ronaldson 1958). The mangrove, however, is purely coastal; inland where kauri grows, lat. 38° S. lies within a region of 25–50 frosts per year (Kidson 1950). Also, Cranwell and Moore (1936) have found kauri trees and saplings growing at an altitude of 800 m, under conditions of frequent frost and occasional hail and snow, yet though they describe damage due to wind, they do not record frost damage. There is a possibility, suggested by McKinnon (1930), that the seedlings may be frost-tender. However, the work described here supports an alternative suggestion, that lower temperatures limit the growth. There appear to be two distinct effects. Firstly, there is a simple decrease in growth rate as temperature decreases below about 24°C. Secondly, kauri seems to become dormant when the average daily temperature maximum falls below 17°C. Data on New Zealand climate (Garnier 1950; Kidson 1950) show that if this were so, the season of growth would be $7\frac{1}{2}$ months (mid Sept. to late Apr.) in Auckland, where kauri occurs naturally, and 7 months in Rotorua, just at the southern limit; but $5\frac{1}{2}$ months in Napier, 5 months in New Plymouth, and 4 months in Taihape and Wellington, where kauri does not occur. Kauri would therefore have a shorter period of growth each year in southern latitudes besides growing more slowly during that time, and would be unable to compete with species better adapted to cool conditions. This would account for the ability of kauri both to grow much further south when not in competition with other species, and to grow at relatively high altitudes, where the temperature range is usually greater than on the corresponding lowlands. In such places, the lower mean temperatures would be offset by the higher maximum temperatures, thus allowing the period of growth to be longer, even though at a slower rate.

(*b*) *Soil Moisture*

The changes in seedling morphology under the various conditions were pronounced. Under dry conditions, material was diverted to root development at the expense of the tops. Root length and root branching showed even greater increases, so that the roots, besides being heavier, were thinner and more profusely branched. In contrast, under waterlogged conditions, despite the relative decrease in root length, there was no change in the root dry weight, so that the roots were thicker and less branched. This implies that although carbohydrate reached the roots under waterlogged conditions, it could not be utilized for extension growth, perhaps through inhibition of either cell division or cell elongation. The direct cause of such root growth inhibition is unknown. Erickson (1946) and Hopkins, Specht, and Hendricks (1950) showed that lowered oxygen tensions had the same effects on root development as flooding. Kramer (1951) also considered that while high carbon dioxide concentrations could be responsible for some effects, the major ones were produced by low oxygen tensions, and suggested that the primary effect was a limiting of translocation. In kauri, carbohydrate transport at least could not have been inhibited significantly, although auxin transport may have been affected.

The lack of any significant effect of waterlogging on seedling mortality is surprising, since such extreme conditions are frequently lethal (Kramer 1949). In comparison with other woody seedling species on which waterlogging experiments have been carried out (*Pinus taeda*, *Juniperus virginiana*, *Taxodium distichum*, *Cornus florida*, and four species of *Quercus*, Parker 1950; *Liriodendron tulipifera* and *Ligustricum japonicum*, Kramer 1951; and *Pinus taeda*, *P. echinata*, and *P. rigida* var. *serotina*, Hunt 1951), kauri as a seedling was at least as tolerant as such flood-resistant species as *P. taeda* and *P. rigida* var. *serotina* (pond pine). Even the mature tree has occasionally been seen growing in permanently swampy ground (Waitakere Ranges, near Auckland, Long, personal communication; Table Mountain, Coromandel Peninsula, Millener, personal communication). Well-developed lenticels on the stem bases of waterlogged seedlings and trees (Cranwell and Moore 1936) may have helped the plants to survive. The behaviour of kauri with respect to the native swamp pine, *Podocarpus dacrydioides*, could be similar to that observed by Hunt (1951), who showed that *Pinus taeda*, though replaced by *P. rigida* var. *serotina* in swamps, was no less resistant towards waterlogging.

There is one possible barrier to establishment. Kauri is autumn-germinating, will not germinate under any layer of soil, and ceases growth at the onset of winter. At this stage it normally has only two cotyledonary and two true leaves; and the 2–5 cm tap-root is completely unbranched. Consequently the wintering seedling is poorly adapted physically to withstand any winter and spring floods. In contrast the native swamp conifer, *Podocarpus dacrydioides*, although shedding its seed in autumn, was found to germinate in late spring, under moderate soil layers, and to form branch roots rapidly.

In the field, seedlings go through a period when they are drought-susceptible. The newly germinated seedlings, dormant during the first late autumn and winter, have a short, unbranched root. On ridge-tops, death of new seedlings through drought in late autumn is quite common, although year-old seedlings are rarely affected seriously. On the other hand, established seedlings have been shown to be able to resist drought and to react to it by a marked stimulation of root development. When boxes of 9-month-old kauri seedlings containing herbs and other seedling species were allowed to dry out, *Lobelia anceps* and *Carpodetus serratus* were dying, *Taraxacum officinale* and *Coprosma robusta* moderately to severely wilted, and *Oxalis corniculata* slightly wilted before *Coriaria ruscifolia* and kauri started to show any effect. Thus except in the very early stages of germination kauri seedlings are drought-resistant, and tolerate a wide range of soil moisture conditions.

This ability to resist drought may be a factor responsible for the occurrence of kauri in greatest abundance on ridge-tops—the first feature of the distribution ever noted for kauri, by Dieffenbach in 1843 and von Hochstetter (1867). The soil factor must also be important; kauri, though affected by poor soils, is extremely tolerant of them. Presumably, like many other conifers (Wilde 1946) it has low mineral requirements, kept even lower by a moderately slow growth rate. In this way it could be confined to poor soils by competition from species better adapted to good soils but intolerant of poor ones.

It was previously shown that under some conditions in the field, kauri seedlings would not establish in high light intensities (Bieleski 1959*a*), although under glasshouse conditions they grew best at the highest intensities (Bieleski 1959*b*); and it was suggested that light was acting through affecting either soil temperature or soil desiccation. Results of the temperature experiments reported here show that while increased soil temperature may have considerably decreased root formation, it was not likely to have affected growth to the extent that the seedlings could not establish. However, solar radiation markedly affects water evaporation from the soil; and the drought-susceptibility of the young seedlings during autumn, when the surface soil layers are most likely to dry out below wilting point (Mirams 1951), suggests that the high light intensity limit to establishment is almost entirely due to this effect. Increased air movement with decreased plant cover (and hence increased light intensity) would contribute to the effect. This would also explain why *Phyllocladus trichomanoides*, growing in the same community as kauri, did not show the same limit (Bieleski 1959*a*), since *Phyllocladus* appears to germinate normally in the spring, when soil desiccation is much less severe. Only the youngest kauri seedlings would be thus affected, since at the end of the first winter rapid root growth commences. The moisture conditions in *Leptospermum* soil are generally constant at depths below 15 cm (Mirams 1951). Thus seedlings once established would be expected to survive changes of cover leading to higher light intensities. The evidence indicated that such changes had occurred. Any factor affecting soil moisture and water evaporation would be expected to modify this higher light intensity limit. It will, therefore, be likely to be different in different communities and even in different areas of the same community.

(*c*) *Soil Mycorrhiza*

The marked increase of seed germination in sterile soil could have been due to heat destruction of germination inhibitors, but this is unlikely since Mirams (1951), despite extensive tests, could not find any evidence for their existence in any of the normal kauri soils or litters. Examination of ungerminated seeds from both sets showed that many seeds from the unsterile boxes were infected with fungi. Some had managed to put out a small radicle before dying. It appears that the soil fungi attacked not only the young seedling (Mirams 1951) but also even the germinating seed. The higher subsequent mortality in the sterile soil was undoubtedly due to the presence of many weak seedlings which normally would not have survived the barrier to successful germination. It was noted that it was largely the weak and spindly seedlings, particularly from seed type B, which died.

Mycorrhizal nodules could not be found on plants from any treatment reported in this paper, yet they occur almost universally on kauri plants found growing in the field. Even though the *Rhizophagus* type of mycorrhiza probably only infects by contact, infection should have been possible. The most probable explanation is that mycorrhiza are decidedly acidophilic (Melin 1953) and the soil used had a pH of 6·8, compared to the pH values in the field of 4·5–6·0. Nevertheless, the results show that mycorrhiza are not essential to the healthy growth of kauri seedlings, at least when the soil pH is high and the soil structure and nutrient status are favourable. In deficient, acid soils mycorrhiza may be necessary, perhaps aiding ion uptake, as in *Pinus virginiana* (Melin, Nilsson, and Hacskaylo 1958). During the course of these studies, root hairs were never seen on the seedling roots (cf. Kozlowski and Scholtes 1948) and it is possible that the ectendotrophic hyphae may function in their stead.

(*d*) *The Soil Factor*

In the past kauri has been considered to be highly tolerant of poor soil (Cheeseman 1914*a*, 1914*b*; Cockayne 1928), and whilst this is true, it can be shown that the growth of the trees is markedly affected by such conditions (Bieleski 1955). Kauri also tends to form its own poor soil, for it produces an acid litter that facilitates leaching, giving a well-developed podzol in a hundred years or so. There is therefore a strong possibility that kauri might, by impoverishing the surface soil, produce conditions unfavourable to kauri seedling establishment or even to maintenance of the stand of kauri. Many workers have noted that kauri often occurs in large, relatively even-aged groves (von Hochstetter 1867; Cheeseman 1914*b*; Hutchins 1918, 1919). These must have come into being over a relatively short period, and subsequent regeneration must have been negligible, since otherwise a heterogeneous mixture of different-aged trees would have resulted. This absence of regeneration was noted by Cheeseman (1914*b*) and Cockayne (1928), who both suggested that light might be the operative factor. Cockayne pointed out that were kauri seedlings light-demanding, they would not be able to establish under any complete forest cover, and therefore that kauri must be a seral community only. However, the seedlings have now been shown to be decidedly shade-tolerant (Bieleski 1959*a*, 1959*b*). In view of the typically low mineral status, acid litter, and strong podzolization of kauri soils, the factors responsible for preventing re-establishment of kauri seedlings may be those of soil structure and particularly root competition. Mature kauri has an extremely well-developed surface rooting system (Yeates 1924; Cranwell and Moore 1936) which can even form a mat of roots under the decomposing litter on top of the soil itself. Where soil has been disturbed under kauri stands, as by milling tractors or roading operations, kauri seedlings will often establish; although changes in light intensity have in the past been generally regarded as the cause. A trenching experiment carried out, apparently by McKinnon, in a non-regenerating stand of kauri resulted in seedlings being able to establish and grow actively (Chapman 1954) (cf. *Pinus* sp., Korstian and Coile 1938; and *Fagus sylvatica*, Harley 1939). Billings (1938) has shown how replacement of conifers by hardwood stands can occur under conditions of strong root competition. Under a pure mature stand of *Pinus echinata*, pine seedling establishment was negligible, mainly as a result of its weak root system, which during the first 4 years lay in the upper 15 cm of soil where root competition was most severe. Young hardwood seedlings (*Quercus* and *Hickoria*), on the other hand, formed strong root systems which soon penetrated below this zone of intense competition. They were thus able to survive and ultimately replace the surface-rooting pines. Kauri is another such surface-rooting species.

Should the failure of kauri to regenerate under its own cover be due to its own soil podzolization and to root competition in the surface layers, there is no reason to suppose that kauri is seral to a hardwood climax. The difficulty in this concept has always been that kauri stands are more abundant than would be expected for a purely seral species. The relationship between the two would seem to be much better explained as a regeneration complex (Poole 1937; Watt 1947) or a case of mosaic regeneration (Richards 1952). On this view, kauri would not be able to regenerate through the unfavourable soil conditions it produces, but would be able to re-invade hardwood stands that replaced it once the soil conditions had changed sufficiently. Recent evidence from the Department of Scientific and Industrial Research (N.Z.) Soil Survey indicates that such may have occurred, and that each cycle may have taken about 1000 years. The stimulus for the development of a new grove can only be guessed. Forest catastrophes with areas felled by wind (Cranwell and Moore 1936; McGregor 1948) or fire could have resulted in such development, but it is doubtful whether these would have been sufficiently frequent. A combination of overmaturity of the dicotyledonous cover, availability of kauri seed, and the occurrence of favourable soil moisture conditions for seed germination (which must always be important because of the autumn germination and low viability of kauri seed) have probably been mainly responsible. Information is now needed on the extent to which kauri regeneration can occur under a dicotyledonous cover.

The whole question of the ecological status of kauri is rendered more complex by the possible occurrence since the 13th century of climatic changes, as postulated by Holloway (1954) to explain certain plant distribution phenomena in forests in the south of New Zealand. Fossil remains found as far south as Otago demonstrate that the distribution has been so affected in the more distant past (Oliver 1953), while some features of the present day distribution suggest that kauri could still be reacting to climate changes. However, unlike the conifers (*Podocarpus* and *Dacrydium* spp.) in the South Island, which are still metastable with respect to the dicotyledons (*Nothofagus* spp.) (Holloway 1954), kauri in the North Island appears to be increasing in importance at the expense of dicotyledons through regeneration following milling. Robbins (1957), who discards Holloway's theory of recent climatic change as an explanation of forest patterns in the North Island, suggests that this is a temporary respite, and that kauri, along with the other conifers, is but the declining relic of an ancient, postglacial podocarp forest, in process of being ousted by broadleaf forests.

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CALLITRICHE IN NEW ZEALAND AND AUSTRALIA

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Summary

A revision of *Callitriche* in New Zealand and Australia shows that 13 species (one with two subspecies) occur in these countries, of which *C. capricorni* (Queensland), *C. petriei* (New Zealand), and *C. aucklandica* (Auckland Is.) are new. *C. palustris* L. (syn. *C. verna* L.) occurs in Victoria only, not as hitherto recorded in New Zealand and widely in Australia. *C. stagnalis* Scop. and *C. hamulata* Ktzg. are adventives in Australia and New Zealand, and *C. heterophylla* Pursh emend. Darby in New Zealand.

C. petriei subsp. *petriei* is the first dioecious taxon found in the genus.

I. Introduction

Callitriche is a cosmopolitan genus with many polymorphic species; individual plants of different species are often very like each other in form. The characters of the fruits are those most useful for distinguishing the species, but fruits are small —less than 2 mm, often less than 1 mm wide. It is not surprising therefore that there has been confusion in its taxonomy and nomenclature. In the European species the confusion dates from Linnaeus's day and authors have resolved it in different ways. In Australia and New Zealand the genus can by no means be said to be well understood. Though five species have been ascribed to Australia by Hegelmaier, the monographer of the genus, writers of Australian floras and compilers of censuses usually give only two species—one only of those given by Hegelmaier and one other. In New Zealand the latest account, that of the first edition of Cheeseman's (1906) "Manual", repeated in the second edition of 1925, is not satisfactory. It is difficult to make determinations with the treatment given. Australian writers of floras seem to have been influenced mainly by Bentham, New Zealand ones by J. D. Hooker and Hegelmaier.

Bentham, in "Flora Australiensis" (1864), writing at a time when Hegelmaier had only recognized *C. macropteryx* Hegelm. (i.e. *C. muelleri* Sond.) in Australia, said: "The genus is found in every part of the globe, and, according to some botanists, consists of but a single species, others divide it into two, the Australian one belonging in that case to the one which has the most universal range. Those who variously extend the genus from 13 to 20 spp. describe the commonest Australian form as endemic." He ascribed all the specimens listed to *C. verna* L., at the same time saying that eastern specimens constituted *C. macropteryx* Hegelm. Australian flora writers for the most part have thenceforward recorded only *C. verna* and *C. muelleri*, save that Black (1926) in the first edition only of his "Flora of South Australia" and Curtis (1956) in "The Student's Flora of Tasmania" recorded *C. stagnalis* and not

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C. verna. In 1928 Williamson, from a critical examination of specimens collected by himself, considered that there seemed to be a few forms distinct enough to rank as separate species, and put his specimens in four groups, of which he compared one to *C. stagnalis* and one to *C. sonderi*. As Hegelmaier's monograph was not available to him he left the four to stand as forms of *C. verna*.

Hooker placed in *C. verna* L. all species except *C. autumnalis* L., as either subspecies or varieties. His remarks on the genus in the New Zealand region are difficult to interpret; they certainly confused Kirk in matters of nomenclature. Kirk and Cheeseman in their floras recognized three species as indigenous to the New Zealand region—*C. verna*, *C. muelleri*, and *C. antarctica*—and a fourth taxon treated as a variety of *C. muelleri*. The position as they give it seemed reasonably clear. Cockayne and Allan (1927: 62), however, wrote under the heading "Exotic Species Wrongly Included in the Flora":

> "6 *Callitriche verna*, L. Possibly there are indigenous varieties of this linneon, but there are almost certainly introduced forms also. The 'species' in New Zealand need closer investigation. According to several informants it has of recent years shown a marked tendency to increase in slow-flowing waters in North Island."

Allan (1940) did not, however, make any mention of *Callitriche* in his handbook of the naturalized flora.

The genus *Callitriche* is one of slender, delicate, glabrous herbs. It is often regarded as purely or mainly aquatic, but many species are amphibious and may grow on muddy shores as well as submerged; a considerable number are terrestrial. Leaves are opposite, almost always entire, and without stipules. Plants are monoecious or rarely dioecious. The flowers are axillary and without a perianth. The female flower consists of two united carpels, but is four-celled by secondary septation; the male consists of a single stamen. Flowers are solitary in the leaf axils, or male and female flowers occur together. In species that are much branched there may also be a leaf bud, the male flower being on the inside near the stem, then outside it the female flower, and outside it again the shoot. Occasionally there are two female flowers or two male flowers in the one axil.

The fruit is four-lobed and breaks up into four one-seeded mericarps, the lobes of which are commonly keeled or angled. The groove seen when the fruit is viewed edge on is that which separates the carpels, the commissural groove (Fig. 1(*b*)), and that seen when viewed face on shows the line of the secondary septum (Fig. 1(*a*)).

C. muelleri shows well most of the features that may be developed in the fruit. It has perhaps the broadest wing of any species. The body of the fruit is brown, the wings paler, whitish brown. In cross section it is seen that the pericarp consists of three tissues: the pale, more or less transparent epicarp, a mesocarp of elongated thin-walled cells on the side walls of which are net-like brown thickenings, and an endocarp of dark-brown cells, much thickened on all but the outer wall. The mesocarp occurs only at the keel of the mericarp, covering only the rim of the endocarp and projecting beyond it. The main part of the endocarp is therefore covered by the epicarp alone. The ripe fruit is brown where the thickened brown walls of the endocarp show through the epicarp, and pale where the pale cells of the mesocarp show.

Most species have these wings consisting of mesocarp cells, though they are lacking in some, e.g. in *C. petriei*. The wing may be one to three cells wide, broad and clearly visible to the naked eye, or narrow and requiring magnification to make it clear. Occasionally, for instance, in *C. hamulata*, where there seems to be no wing of mesocarp tissue, there is apparent at the edge of the mericarp, when viewed face on, a narrow border. This border is due to a view of more or less transparent epicarp tissue without mesocarp tissue behind it and it may vanish from sight as such when the fruit is viewed edge on, e.g. as it does in *C. antarctica*. For descriptive purposes, in this paper the term "wing" is used when a border is seen in face view, whether or not there is an actual wing of mesocarp tissue. Sometimes, as often in *C. umbonata*, the epicarp breaks up and slips off, leaving the wing attached to the endocarp.

When the fruit of *C. muelleri* is viewed face on after the epicarp and the seed have been removed by treatment with potassium hydroxide, there is seen a criss-cross pattern of brown ridges of thickening on the inside wall of the endocarp cells. The thickening in each cell lies in line with that of the neighbouring cells, so that continuous lines of thickening run right across the face of the mericarp. This type of criss-cross thickening is paler and less well developed in some species, and entirely lacking in others.

Hegelmaier (1867: 5–7) described brown ridges of thickening on the lateral and outer walls of the endocarp layer of *C. muelleri*, and states that such thickenings in other species may be less well developed or absent. Such thickenings are not readily observed by the methods used in this study. Thickenings which may be on the cell walls of the wings are, however, visible under magnifications of about ×35–50 when the epicarp has been stripped off.

It should be said here that Schotsman (1954: 360) adopts the opinion of Wahlenberg that it is the seeds, not the fruits, which are winged. This implies that what are here called mesocarp and endocarp and are regarded as part of the carpel are in fact derived from the ovule, that what are here thought to be in the nature of pyrenes are in reality seeds. On the other hand Fassett, as he shows by a description and a figure of a cross section of the seed coat of *C. heterophylla* (1951: 139, Plate 1173), regards the hard, thick-walled tissue as carpellary. The fact that the endosperm and embryo in the young fruit of *C. muelleri* is enclosed in what seems to be a thin testa, supports his view.

For studying fruits the method which was originated by Fassett and fully described by him in his work on *Callitriche* (1951: 141–2) was used. Whole fruits, half fruits to show the commissural groove, cross sections of fruits, and the pericarps and wings of fruits were mounted on small cellulose acetate slides by means of a drop of acetone.

Habit and vegetative characters, with much justification, are generally regarded as unreliable for determination of *Callitriche* species, but they are not without some use. Plants from the main islands of New Zealand, when well developed, can often be identified by their leaf shape and venation alone. Many of the species in Australia, however, are too alike in habit and leaf form to be so identified, but *C. muelleri* almost always, *C. stagnalis* frequently, and sometimes *C. sonderi* are identifiable by vegetative features.

The simplest leaf is linear with a single vein. In broader leaves the venation is better developed. The basic pattern appears to be a midrib running to the tip or almost to the tip of the leaf, together with two side veins which arise from the midrib and which arch around and meet the midrib near the top, opposite or nearly opposite each other. The largest leaves and rosette leaves often have veins additional to these: sometimes there is a second or third series of looped veins outside the first (for convenience in the description these are herein called nerves); sometimes there are free veins arising from the midrib or side nerves.

TABLE 1

CHARACTERS OF POLLEN OF SPECIES OF CALLITRICHE

Species	Size (μ)	No. of Apertures	Exine Pattern	Type of Aperture
C. antarctica	27	3–6	Baculate	Generally long broad furrows but sometimes almost circular
C. aucklandica	25	3–6	Clavate	Large, more or less circular
C. petriei	20	3(4)	Baculate	Indistinct, half length of grain, tapering
C. petriei subsp. *chathamensis*	19	3(4)	Baculate	Zone of weakness
C. cyclocarpa	18	3	Verrucate	Large, more or less circular
C. muelleri	17	3?	Clavate	Zone of weakness
C. stagnalis	17	0	Baculate	Zone of weakness
C. heterophylla	16	0	Verrucate	Zone of weakness
C. brachycarpa	30*	0?	Baculate	Zone of weakness

*Treated by acetolysis method.

To study the venation, several leaves of a specimen were placed in 5 per cent. potassium hydroxide for 18 to 24 hr till cleared and bleached, then rinsed in water and mounted in 90 per cent. alcohol between two glass microscope slides. The slides were placed in a photographic enlarger set for a magnification of ×4 and the outlines of leaf and veins traced on a piece of white card.

The information provided by Mr. N. T. Moar shows that the pollen of each species is distinctive, that is, so far as known from the pollen available. Unfortunately there was little or none on specimens of most of the Australian species.

The pollen is aperturate, with a thin intectate exine about 1 μ in diameter. The characters for each species are given in Table 1. Pollen of all species was mounted direct in glycerine jelly, except that of *C. brachycarpa*, which was treated by the acetolysis method and the size of which therefore cannot be compared with that of the others.

The apertures are not always easily recognized, because the grains tend to be collapsed or over-expanded according to the particular method used in preparation. In several species well-defined apertures are absent, there being instead rifts or "zones of weakness" in the exine which are presumed to function as apertures.

II. Intrageneric Relationships

Fassett (1951) described the section *Microcallitriche* for the broad-fruited, subterrestrial species. In *Microcallitriche* he put eight American species and remarked that a few species are found in Japan, Australia, and New Zealand, but did not specify which. Characters by which he distinguished the section are the palustral or subterrestrial habit, the subuniform leaves, the absence or rarity of peltate hairs, the lack of bracts, the narrowness of the anthers (0·1–0·2 mm broad), the shortness of the stamens (0·2–1·2 mm long), the shortness of the stigmas, and the fact that the fruit is broader than long.

Hegelmaier (1867: 7–8) had already considered whether the terrestrial species of Australia and America should be placed in a separate section or not and had decided against it. For the most part he considered characters other than those chosen by Fassett. He noted that calcium oxalate crystals occur in the inner layer of the pericarps of many of the subterrestrial species, that the keel cells of the fruit have a network of ridges well developed, that the bracts are absent, and (in a key) that the filaments of the anthers are not lengthened after flowering.

The distinction between the two sections, however, is by no means so clear cut as might be desired. Hegelmaier pointed out that calcium oxalate crystals are not present in all terrestrial species, nor for that matter consistently in any species; there is every gradation in the thickening of the cell walls of the fruit in the terrestrial species and no distinct break from conditions in the amphibian species. The greatest obstacle to making a division he found, however, to lie in the existence of *C. umbonata*. This species in the characters of the wing of the fruit is very close to *C. muelleri*, a plant in which the features typical of the terrestrial species are strongly developed. Also, umbones, which are prominent at the base of the fruit of *C. umbonata*, occur otherwise only in *C. sonderi*, *C. peploides*, and *C. occidentalis*—all terrestrial species. Yet *C. umbonata* usually grows in water and has the habit common in the amphibian group; it lacks oxalate crystals.

The presence or absence of bracts is not a satisfactory distinguishing feature. *C. sonderi* and *C. capricorni*, which by habit, fruit character, and stamen size should unquestionably be included in *Microcallitriche*, both have bracts. They are usually lacking in *C. hamulata*, *C. pedunculata*, *C. antarctica*, and *C. aucklandica*, and have not been seen at all in *C. petriei*, species which should all, from the character of the stamens, be classed as members of the section *Callitriche*. It is true that *C. umbonata*, so far as its characters are known (stamens for all practical purposes are lacking on the specimens seen by me), clearly falls in the section *Callitriche* as Fassett defines it. But there is *C. brachycarpa* to be considered. This is a terrestrial species of which the habit and fruit characters are those of *Microcallitriche*, yet the stamens are like those of the section *Callitriche*, bracts are sometimes present, and stellate hairs very common.

On the whole it seems better to adopt Hegelmaier's attitude, and, while recognizing the affinity of the terrestrial species, refrain from separating them as a distinct section. If the subsection *Microcallitriche* is accepted its description must be amended by the omission of the statement that bracts are absent.

The species in Australia and New Zealand could then reasonably, though still not entirely satisfactorily, be placed as follows:

CALLITRICHE: *C. antarctica*, *C. aucklandica*, *C. petriei*, *C. heterophylla*, *C. palustris*, *C. stagnalis*, *C. hamulata*, *C. cyclocarpa*, *C. umbonata*.

MICROCALLITRICHE: *C. brachycarpa*, *C. capricorni*, *C. sonderi*, *C. muelleri*.

III. INDIGENOUS AND NATURALIZED SPECIES

Cockayne and Allan (1927), as mentioned earlier, queried whether any of the forms of "*Callitriche verna*" in New Zealand were entirely indigenous, and it is open to doubt whether those species not endemic to Australia and New Zealand are in fact native.

C. hamulata is native to Europe and Greenland, and as it was first collected in Australia in 1911 and in New Zealand in 1956 and is not recorded in regions between these countries and Europe, it is without doubt introduced.

C. palustris and *C. stagnalis*, however, are indigenous in areas much closer to Australia and New Zealand. There is more reason to suppose they might be native. Both occur in the Himalayan region in Asia and in New Caledonia, though whether they are indigenous to the latter country is not clear. *C. palustris* has also been recorded for New Guinea.

The earliest dated collection of *C. palustris* for Australia is Mueller's from "springs on the lower Hume's River", i.e. in the Albury district, in January 1874. Mueller passed through this district at that date on his way to the Australian Alps (McBarron 1955). In the period of almost 40 years between the commencement of settlement of the district in 1835 and Mueller's visit there was plenty of time for an aquatic such as *C. palustris* to be introduced and established. On the other hand, as *C. palustris* has an extremely wide range—throughout North America north of latitude 30° N., in Europe, Asia, and the mountains of New Guinea—the possibility of its being indigenous in south-eastern Australia cannot be entirely ruled out.

C. stagnalis is probably introduced in Australia. The earliest dated collection seen is that of Betche from Sydney in 1881. The earliest from Victoria is one from Rosstown in 1902. In contrast, *C. muelleri* was collected as early as 1843 in New South Wales and 1854 in Victoria; *C. umbonata*, *C. sonderi*, and *C. brachycarpa* before 1854; *C. cyclocarpa* before 1868. *C. stagnalis* is as conspicuous a plant as any of these, indeed more conspicuous than most of them, yet Mueller, who gathered six of the species and made 10 or 11 collections of *Callitriche*, did not collect it. There seems no reason to regard it as other than introduced to Australia.

It is undoubtedly *C. stagnalis* that Cockayne and Allan regarded as "almost certainly introduced" in New Zealand.

The earliest mention of *C. stagnalis* as such in New Zealand is by Hooker in 1867, but it would be rash to assume that he had seen authentic specimens from

New Zealand. In the "Flora Antarctica" (1845: 54–5) he indicated that there were two forms of *Callitriche* in the Campbell Islands, one *C. verna* and one its variety, *terrestris*. In 1852 in "Flora Novae Zelandiae" he refers to "Flora Antarctica" but under "var. β" he gives a brief description and refers to it the "*C. tenella*" of "Banks & Sol. Mss.". The description fits *C. tenella* (i.e. *C. muelleri*) better than any other species Hooker might be supposed to have been considering, though it can scarcely be called an adequate description of the plant. He gives as a habitat: "abundant in deep still, and running water; also in pools, and on wet ground, Banks and Solander, etc.", which is not true for *C. muelleri*, a typical terrestrial species. In the "Handbook of the New Zealand Flora" (1867) he merely gives "*C. verna*" and states that it is "common in wet soil and watery places throughout the islands, Banks and Solander, etc. Lord Auckland's group and Campbell's Island, J.D.H.". The statement that "*C. verna*" is common throughout the islands is curious. Solander mentions only one collecting place in New Zealand for the genus. For his own collecting Hooker gives his own initials for the subantarctic islands only. The "etc." adds nothing, for it invariably appears after Banks and Solander's names and appears merely to acknowledge the presence and possible collecting activities of other members of the expedition. Richard, Cunningham, and Raoul do not mention the genus. Hooker may have had in mind those collections of which Colenso wrote (1888: 190) when he said of *C. verna* and its variety that "I, myself had early collected and sent specimens of those plants to Kew". Did Hooker see these before 1867 and fail to mention them? In the additions to the "Handbook" Hooker wrote: "*Callitriche verna*—This is the form or species called *C. stagnalis*, Scopoli (*C. platycarpa*, Kuetzing), and is *C. verna* of Linnaeus, distinguished by the broad thick wings of the fruit, and broad short leaves." We may ask: what was he placing in *C. stagnalis*? The specimens he had up till then mentioned were those of Banks and Solander from New Zealand itself, and his own from the Auckland and Campbell Islands, and he gives no indication that he did not mean all these to be considered as *C. stagnalis*. Hooker's specimens from Campbell Island are *C. antarctica*; Banks and Solander's specimen is *C. muelleri*. If Hooker was thinking of Colenso's specimens he did not say so. Kirk was not right in considering that *C. muelleri* and *C. stagnalis* are synonymous but he may well have been right if he supposed Hooker to think Solander's *C. tenella* to be synonymous with *C. stagnalis*. If such was Hooker's supposition, his statement has no value as evidence for *C. stagnalis* being indigenous to New Zealand. The European "*C. verna*" that Solander mentions in his manuscript as growing along with his *C. tenella* at Motuaro, might perhaps have been *C. stagnalis*, but it might equally as well have been *C. petriei*. There are no specimens in the British Museum of this "*C. verna*", and presumably Banks and Solander did not collect a specimen of what they regarded as a common European species.

The earliest dated herbarium specimen in New Zealand is that of Petrie from Epsom, Auckland, 1889. There are undated specimens, however, which could be earlier: that of Kirk from the Waikato River near Churchill, which could have been collected in 1869, 1870, or 1872; and that of Cheeseman, also from the Waikato, which could have been collected in 1884. According to Thompson (1922: 369) the adventive species *Nasturtium officinale* was abundant in the Waikato River by 1872, and this being the case there is no reason to regard a record of the same date and place as showing *C. stagnalis* to be indigenous.

Kirk's statement (1872: 257): "*Callitriche verna*, L. I have not seen specimens of the typical form. Our plant is *C. muelleri* which resembles the British *C. platycarpa*, Kuetz., but is not identical with any European form. It is probably common throughout the islands."—does not help, seeing that he identified at least one obvious specimen of *C. stagnalis* as *C. muelleri* and that he also stated (1873: 324): "The Ohau stream, which connects Rotorua with Rotoiti, contained masses of *Myriophyllum variaefolium*, *Potamogeton* n.s. *Callitriche muelleri*, *Azolla rubra*, *Lemna minor*, etc." It is most improbable that *C. muelleri*, a terrestrial species, was found in such a habitat. The plants in question may have been *C. stagnalis* or *C. petriei*.

The fact that "*C. verna*" was supposed to have shown a marked tendency to increase in slow-flowing waters of the North Island may be due to the fact that it is an exotic and was still increasing its range, or it may merely reflect habitat changes due to settlement—perhaps decreased shade, greater silting, and increased fertility from run-off from manured country. *C. stagnalis* has not been collected in remoter parts of the country such as Lake Duncan and Lake Katherine in Fiordland, where *C. petriei* occurs. It could have been introduced at least as early as *Nasturtium microphyllum* and *Elodea canadensis*, water plants which were spreading in Canterbury in 1868, 18 years after the founding and main settlement of the province. The probability is that it is introduced.

IV. MATERIAL

(*a*) *Specimens Seen*

Specimens from the following herbaria were examined: the National Herbarium of Victoria (MEL), the Queensland Herbarium (BRI), the National Herbarium of New South Wales (NSW), the State Herbarium, Western Australia (PERTH), the State Herbarium of South Australia (AD), the Auckland Museum (AK), the Dominion Museum (WELT), the Canterbury Museum (CANTY), and the Botany Division, Department of Scientific and Industrial Research (CHR).

The specimens of the Cape Expedition (CAPE EXPEDN) are at present in the Botany Division, D.S.I.R.

Some 21 specimens without fruits, nearly half of them from the subantarctic islands, were not identifiable.

(*b*) *Types*

The Hegelmaier Herbarium, including the Australian specimens on which Hegelmaier based his new species, is in the Staatliches Museum für Naturkunde, Botanische Abteilung, Tübingen (STU), and there are duplicates of these in the National Herbarium of Victoria. Dr. Faber of the Museum has kindly provided a description of the labels of the types. It is evident that there are some differences between the wording of the labels of the Hegelmaier Herbarium and the wording on the Melbourne specimens, and between the herbarium labels and what Hegelmaier published. As the number of these early collections is so few, the collectors only two, and the localities distinct, there is fortunately little difficulty in correlating published statement with herbarium specimens.

Some type specimens, according to records, should be in the Vienna Natural History Museum (W) and the Stockholm Museum (S).

As I have seen only isosyntypes of *C. brachycarpa* and *C. umbonata* I have not chosen lectotypes of these names.

V. TAXONOMY

Synonyms for the introduced species are here given only when they have been used in reference to Australian or New Zealand material.

KEY TO THE GENUS CALLITRICHE IN AUSTRALIA AND NEW ZEALAND

1. Fruit broader than long 2
   Fruit not broader than long 9
2. Leaves rhomboidal, apiculate, usually with a single tooth on either side; wing one-third width of the mericarp .... **1.** *C. muelleri*
   Leaves not as above; wing if present less than one-third width of mericarp 3
3. Bracts not or rarely present; styles more than 1 mm long; fruit not thicker at the base than above 4
   Bracts present; style 0·2 mm or less long; fruit much thicker at the base than above 8
4. Leaves fleshy, anthers 0·5–1·5 mm broad, filaments tapering from a broad base 5
   Leaves thin, anthers 0·3–0·5 mm broad, filaments not tapering 6
5. Fruit rounded on the edge, commissural groove narrow and shallow .... **6.** *C. antarctica*
   Fruit keeled, winged, commissural groove wide, deep, and sharp .... **7.** *C. aucklandica*
6. Fruit narrowly winged, with a broad sinus; plant terrestrial .... **4.** *C. brachycarpa*
   Fruit with rounded lobes, not winged; plant amphibious .... **8.** *C. petriei*
7. Dioecious, leaves 1·1–5 mm long .... **8a.** *C. petriei* subsp. *petriei*
   Monoecious, leaves 2·5–8 mm long .... **8b.** *C. petriei* subsp. *chathamensis*
8. Mericarps umbonate at the base, commissural groove narrow .... **2.** *C. sonderi*
   Mericarps not umbonate, commissural groove very wide .... **3.** *C. capricorni*
9. Lower, earlier leaves 3-nerved, linear-spathulate to spathulate 10
   Lower, earlier leaves 1-nerved, linear 12
10. Upper, later leaves 3-nerved, sometimes with free veins, bracts rare or absent .... **6.** *C. antarctica*
    Upper, later leaves 3- to 7-nerved, no free veins; bracts conspicuous 11
11. Fruit round, more than 1 mm in diameter, conspicuously and evenly winged all round .... **10.** *C. stagnalis*
    Fruit less than 1 mm long, winged at top only .... **9.** *C. heterophylla*
12. Fruit thicker at the base than above 13
    Fruit not or scarcely thicker at the base than above 14
13. Fruit 1 mm or more long, conspicuously winged, umbonate at the base .... **5.** *C. umbonata*
    Fruit less than 0·9 mm long, scarcely winged, not umbonate .... **12.** *C. cyclocarpa*
14. Style erect, conspicuous bracts present; fruit noticeably longer than wide .... **13.** *C. palustris*
    Style deflexed; bracts infrequent and inconspicuous; fruit almost circular .... **11.** *C. hamulata*

1. C. **muelleri** Sond., Linnaea **28**: 229 (1856).

Figs. 1, 1*A*

Type.—Latrobe R., Vic., *F. Mueller*, May 1853 (holotype presumably in Sonder's Herbarium (S)).

C. macropteryx Hegelm., Monogr. Callitr., 59 (1864). Type: Hawkesbury R., *F. Bauer* (W).
C. microphylla Colenso, Trans. Proc. N.Z. Inst. **20**: 190 (1888). Type: Dannevirke, County of Waipawa, *W. Colenso*, 1887 (AK, WELT).

Fruit.—Very shortly stalked, ferruginous, broader than long, 1·2–1·4 mm broad by 1·1–1·2 mm long (usually 1·3 by 1·1 mm), obcordate or oblong, winged, wing very broad and conspicuous, membranous, crisped, pale or whitish; facial groove shallow, narrow, and straight, commissural groove deep. *Flowers.*—Usually a male and female together in one axil, ebracteate; styles short, *c.* 0·05 mm long, lengthening to 0·15 mm in young fruit, erect, soon falling; stamens with short filaments, *c.* 0·25–0·3 mm long, not lengthening as the fruit ripens, much shorter than the ripe fruit; anthers *c.* 0·1 mm wide; pollen grains 17 μ in diam., 3? "zones of weakness", exine pattern clavate. *Plant.*—Prostrate, branching, delicate, light green, usually terrestrial on damp soil in shade; monoecious. *Leaves.*—Characteristically rhomboidal, petiolate 2·5 mm long by 1·5 mm broad to 7·5 by 4·8 mm, blade broader than long and cuneate at base, apiculate, with a small single tooth on either side, nerves 3–5 with a free vein running to either tooth; earlier leaves often not as markedly rhomboidal, without teeth, with simpler venation.

General Distribution.—Eastern Australia south of latitude 17° S., from the Dividing Range to the coast; Kermadec Is.; New Zealand north of latitude 42° S.

Specimens Seen

AUSTRALIA—QUEENSLAND: Atherton, E. Betche, Aug. 1901 (NSW); Burnett R., *J. Keys*, Aug. 1889 (MEL); Burnett R., no collector, Aug. 1889 (NSW); Blackall Ra., *C. T. White*, 31.viii.1921 (BRI); Archer's station,* *Leichhardt*, 28.viii.1843 (NSW); Nundah Ck., Virginia, *C. T. White*, 16.ix.1916 (BRI); Brisbane R., *F. M. Bailey*, July 1874 (BRI); prope Brisbane R., *A. Dietrich*, 1863–1865 (BRI); Brisbane R., *F. Mueller*, July 1855 (MEL); Tweed, S. of Coolangatta (MEL); Taylor's Ra., no collector or date (BRI). NEW SOUTH WALES: New South Wales, no collector or date (NSW); New South Wales, *Leichhardt*, 1843 (MEL); Doyle's Rd., *c.* 48 miles W. of Wauchope, *J. Garden*, 4.x.1951 (NSW); Upper Williams R., *L. Fraser and J. Vickery*, 13.i.1934 (NSW); Blue Mts., no collector or date (MEL); Blue Mts., *Woolls* (MEL); Blue Mts. from Kurrajong, *Atkinson* (MEL); Port Jackson district, *R. Fitzgerald*, 1888 (NSW); Port Jackson district, *J. H. Camfield*, Nov. 1897 (NSW); Thirroul, *A. H. S. Lucas*, Jan. 1917 (NSW); Yellow Rock Ck., Albion Park, *E. J. McBarron* 1576 (NSW). VICTORIA: Tributary of Gellibrand R., *H. B. Williamson*, 15.iv.1903 (NSW); affluent of Gellibrand R., Irrewillipe, *H. B. Williamson*, April 1903 (MEL); Gellibrand R. near Colac, *H. B. Williamson*, 14.i.1903 (MEL); Otway Ra., *Williamson* (MEL); Otway Ra., *H. B. Williamson*, April 1903 (MEL); Wallace Ck., Tonimbrook, *J. H. Willis*, 26.ii.1936 (MEL); Latrobe R., *F. v. Mueller*, May 1853 (MEL, isotype); on overflowed places along Latrobe R., *F. v. Mueller*, 20.iv.1853 (MEL); Snowy R., *F. Mueller*, Feb. 1855 (MEL); near Mt. Ellery, *E. Merrah*, 1886 (MEL); between Bemm R. and Coombinbah R., *W. A. Sayer*, 1887 (MEL); Cann, *H. B. Williamson*, Feb. 1887 (MEL); East Gippsland, *Merrah* (MEL).

*Though the label says, "Archer's Station is the modern Gracemere, near Rockhampton Q", the Archer's Station that Leichhardt visited was "Durundur" between Caboolture and Woodford about 30 miles north of Brisbane (see Blake, Proc. Roy. Soc. Qd. **66**: 10–12 (1955)).

NEW ZEALAND—KERMADEC ISLANDS: *T. F. Cheeseman*, July 1897 (AK); Tui Lake, Crater, Sunday I., *W. R. B. Oliver*, Oct. 1908 (WELT). THREE KINGS ISLANDS: Great I., *G. T. S. Baylis*, 21.ii.1934 (AK); Great I., *G. T. S. Baylis*, 4.xii.1945 (AK). NORTH ISLAND: Spirits B., *L. B. Moore*, 1.i.1954 (CHR); Kaiaka, Mangonui, *H. Carse*, Dec. 1921 (CANTY); Kaiaka, Mangonui, *H. Carse* (CANTY); without collector or date (AK 2629, 2243); Bay of Islands, *S. Berggren*, Oct. 1874 (WELT); Bay of Islands, *T. Kirk* (WELT); Bay of Islands, no collector, date, or number (WELT); Wara Wara State Forest, *R. Cooper*, 25.xi.1949 (AK); Waipoua Kauri Forest, *R. Cooper*, 24.xi.1949 (AK); Waipoua Forest, *R. Mason and N. T. Moar* 125 (CHR); Waipoua Forest, *R. Mason* 872 (CHR); Maungatapere, near Whangarei, *H. Carse*, 3.x.1897 (WELT); Maungatapere, near Whangarei, *H. Carse*, 22.ix.1897 (CANTY, AK); Parua B., Whangarei Hbr., *D. Petrie*, Nov. 1901 (WELT); L. Ototoa, South Kaipara Head, *N. T. Moar* 559 (CHR); Whangaripo Valley, Rodney Co., *D. Petrie*, Nov. 1919 (WELT), *D. Petrie*, Nov. 1920 (WELT); Great Barrier I., *T. Kirk*, Dec. 1867 (WELT); Great Barrier I., *R. Mason* 493 (CHR); Warkworth, *L. B. Moore*, 27.xii.1950 (CHR); Kawau, no collector or date (WELT); Little Barrier I., *J. Adams*, Jan. 1901 (AK); Moehau, Coromandel Peninsula, *D. Petrie*, Jan. 1899 (WELT); Auckland, *T. F. Cheeseman* (AK); Auckland, T. Kirk's herbarium (WELT); Auckland, *T. Kirk* (CANTY); Western Springs, Auckland, *T. Kirk*, 18.ii.1865 (WELT), *T. Kirk* (AK); Titirangi, near Auckland, *H. Carse*, 22.v.1922 (CANTY), *D. Petrie*, 11.xi.1912 (WELT); Oroua R., *I. W. Davey*, 15.iv.1937 (CHR); Pohangina Valley, *F. Duguid*, 23.iii.1952 (CHR); watercourses near Dannevirke, *W. Colenso*—type material of *C. microphylla* (AK, WELT); near Ohau, Tararua Ra., *F. Duguid*, Aug. 1951 (CHR); Maungakotukutuku Stream, Tararua Ra., *V. D. Zotov*, 5.iii.1933 (CHR); Wallaceville Animal Research Station, *A. J. Healy* 52/72 (CHR); Gollan's Valley, Wellington, *R. Mason* 1469 (CHR). SOUTH ISLAND: Westport, *R. Mason and N. T. Moar* 1709 (CHR); Westport Domain, *R. Mason and N. T. Moar* 1721 (CHR).

C. muelleri is one of the most distinct members of the genus. No other species has fruit so broadly winged or a leaf of so distinctive a shape; it appears to be the only species to develop teeth on either side of a broad leaf.

It was first collected by Banks and Solander from near Motuaro* and described in manuscript by Solander as *C. tenella*. Apparently it was next collected by the Forsters, for Savage (1945: 1) states that there is in the Linnean herbarium a specimen of *Callitriche* from Otaheite labelled *C. tenella* by the younger Linnaeus. This is no doubt a specimen in the set of duplicates of the Forster collection, which according to Merrill (1954) was bought by Abraham Baeck and ultimately found its way into the herbarium of the younger Linnaeus. Drake del Castillo (1893), however, does not record any species of *Callitriche* from Tahiti and I have seen no other reference to any member of the genus being there.

Hegelmaier (1867: 11) recognized without question that his *C. macropteryx* was identical with Sonder's earlier *C. muelleri*, which he appears to have overlooked before, and thenceforward he accepted Sonder's name. In New Zealand Kirk and Cheeseman likewise regarded *C. macropteryx* as merely a synonym for *C. muelleri*, and Australian botanists on the whole would seem to have done the same. Colenso was evidently unaware of any literature dealing with *Callitriche* in Australasia, other than Hooker's "Botany of the Antarctic Voyage", when he described specimens of *C. muelleri* as a new species, *C. microphylla* (Colenso 1888: 190–1). His description is full and clear and it is a pity more use was not made of it by Cheeseman. In Europe, however, Pax and Hoffman (1931: 239) separated the two species on the ground that the base of the fruit is strumose in *C. macropteryx*—though this is not mentioned in the original description—but not in *C. muelleri*. *C. muelleri* they give for southern Australia only, *C. macropteryx* for New Zealand only, in spite of the fact that the type of *C. macropteryx* is Australian. It is true that occasionally a fruit of *C. muelleri* has the base of the mericarp at the inner edge turned out somewhat, but scarcely enough to call it strumose, and it is merely a trifling difference that does not occur consistently even on the one plant. There is no doubt that *C. macropteryx* is identical with *C. muelleri*.

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*In the Bay of Islands. On Plate XVI of the Charts & Views which accompany Cook's Journal (ed. Beaglehole 1955) there is "A VIEW of the ISLAND MOTUARO lying in the BAY of ISLANDS." From Beaglehole's footnotes on pages 214 and 215 it is clear that this is the name used by Banks for the island now known as Motu Arohia. There is a Motuara Island in Queen Charlotte Sound opposite Ship's Cove. This is the Motu-ouru Island of Cook's Journal (ed. Beaglehole 1955: 242), and the Hippa Island of his Chart on Plate XVII. No doubt it led Cheeseman (1925) to attribute several of the species collected by Banks and Solander to Motauru, Queen Charlotte Sound, but the locality for all the Banks and Solander specimens from the Bay of Islands is given as Motuaro by Solander in his manuscript, and that for the Queen Charlotte Sound specimens as Totaranui.

The only reliable evidence of the species from the South Island is the specimens of R. Mason and N. T. Moar Nos. 1709 and 1721 from Westport in 1953, for although in Kirk's and Cheeseman's Floras its distribution includes the South Island and Stewart Island, and although its name is included in some South Island floristic lists, there were no specimens in New Zealand herbaria that substantiated these statements. It seems unlikely that it grows in Otago and Southland. Though in the North Island it occurs from the far north to near Wellington, it appears to be more abundant in the north. Its apparent absence from the lowlands of the middle North Island may be due to the fact that there have been fewer collectors there.

Although Oliver (1910: 136) says that *C. muelleri* at Tui Lake in the Kermadec Islands grew "either entirely submerged or on the bank close by the water's edge", it is typically a terrestrial species of damp soil and places subject to occasional inundation.

2. **C. sonderi** Hegelm., Verh. bot. Ver. Brandenb. **9**: 18–19 (1867).

Figs. 2, 2*A*

Type.—"In paludibus prope Station peak Austr. felix. Dr. F. Müller in Herb. Sond." (presumably in Sonder's Herbarium at Stockholm).

Fruit.—Dark brown, minute, broader than long, 0·7 by 0·5 mm, base of mericarps at inner edge thick and pushing against each other so that the fruit is conspicuously strumose, keeled and slightly winged, commissural groove very narrow and shallow. *Flowers.*—Male and female flowers together in axils of both leaves; bracts present, narrowly triangular to linear, 0·2–0·3 mm long; styles very short, 0·1–0·2 mm long, upright, persistent; stamens about 1 mm long. *Plant.*—Terrestrial, low, creeping and matted. *Leaves.*—Very small, linear-obovate, 3-nerved, sometimes with 2 short free veins arising from the midrib, about 1·5 mm long by 0·5 mm wide.

General Distribution.—Eastern half of Australia south of latitude 25° S., mostly in the inland regions.

Specimens Seen

AUSTRALIA—QUEENSLAND: Bundaberg, *J. Keys* (BRI 154). NEW SOUTH WALES: L. Cobham, near Milparinka, *W. Bäuerlen*, ex Herb. H. B. Williamson (MEL); L. Cobham, *W. Bäuerlen*, Sept. 1887 (MEL); Darling R., near Bourke, *E. Betche*, Oct. 1883 (MEL; NSW 33817); Lower Darling R., *Mrs. C. E. Holding*, 1888 (MEL). VICTORIA: Mildura, *H. B. Williamson*, Sept. 1912 (NSW 33819); Mildura, *J. M. M.* ex Herb. H. B. Williamson, Sept. 1912 (MEL); L. Little Hattah, Kulkyne National Forest, *J. H. Willis*, 6.ix.1941 (MEL); L. Hattah, *H. B. Williamson* (MEL). SOUTH AUSTRALIA: Cardillo Downs, *J. B. Cleland*, May 1924 (AD); Loxton, Upper Murray Mallee, *Hj. Eichler* 12328 (AD).

Unfortunately the isotype does not seem to be now in the *Callitriche* collection at the Melbourne Herbarium. However, there seems little reason to doubt the identification of the specimens here attributed to *C. sonderi*. They agree with Hegelmaier's amended description in every respect. Hegelmaier originally described the plant as not having bracts but later noted that he had occasionally found them. They are scarce and easily overlooked on specimens with mainly mature fruits, and appear to be deciduous. Williamson matched his Mildura and Lake Hattah specimens and those of Bäuerlen from Lake Cobham with Mueller's type collection, and called them *C. sonderi*. The fruits are very distinct and the small leaves characteristic; Williamson is unlikely to have been mistaken.

3. C. **capricorni** sp. nov.

Figs. 3, 3*A*

Holotype.—Brisbane R., *F. M. Bailey*, July 1874 (BRI 151).

Planta terrestris floribus bracteis triangularibus, fructibus ferrugineis latioribus quam longis (0·7–0·85 mm latis, 0·5 mm longis) faciebus planis basi multo crassioribus quam apice, conspicue alatis ala brunnescenti, basique sinu praeditis; commissura (transversim secta) latissime breviterque V-formi.

Fruit.—Dark brown when ripe, much broader than long (0·7–0·85 mm broad by 0·5 mm long), faces flat, much thicker through at base than at top, evenly winged with fairly wide, brown wing; top and bottom of each mericarp rounded so that there is a sinus at top and bottom; commissural groove very wide and shallow, V-shaped, much wider at the base than at the top. *Flowers.*—Both male and female flowers together in the axils of both leaves; bracts triangular, blunt, *c.* 0·2 mm long; styles very short, 0·1 mm; stamens 0·3–1·5 mm long. *Plant.*—Terrestrial, creeping, matted. *Leaves.*—Spathulate or obovate, 3-nerved, sometimes with free veins on the midrib and outer side of the outer nerves.

General Distribution.—Australia—Queensland.

Specimens Seen

AUSTRALIA—QUEENSLAND: Gracemere, *P. O'Shanesy*, 20.viii.1867 (MEL); Brisbane R., *F. M. Bailey*, July 1874 (BRI 151, holotype).

C. capricorni appears to resemble most closely *C. deflexa* A. Br. ex Hegelm. of America, but *C. deflexa* lacks bracts and there is no indication that the fruit is thicker at the base than at the top. The only other Australian species with such small fruit, much broader than long, is *C. sonderi*, but the fruit of *C. sonderi* is quite distinct in other respects.

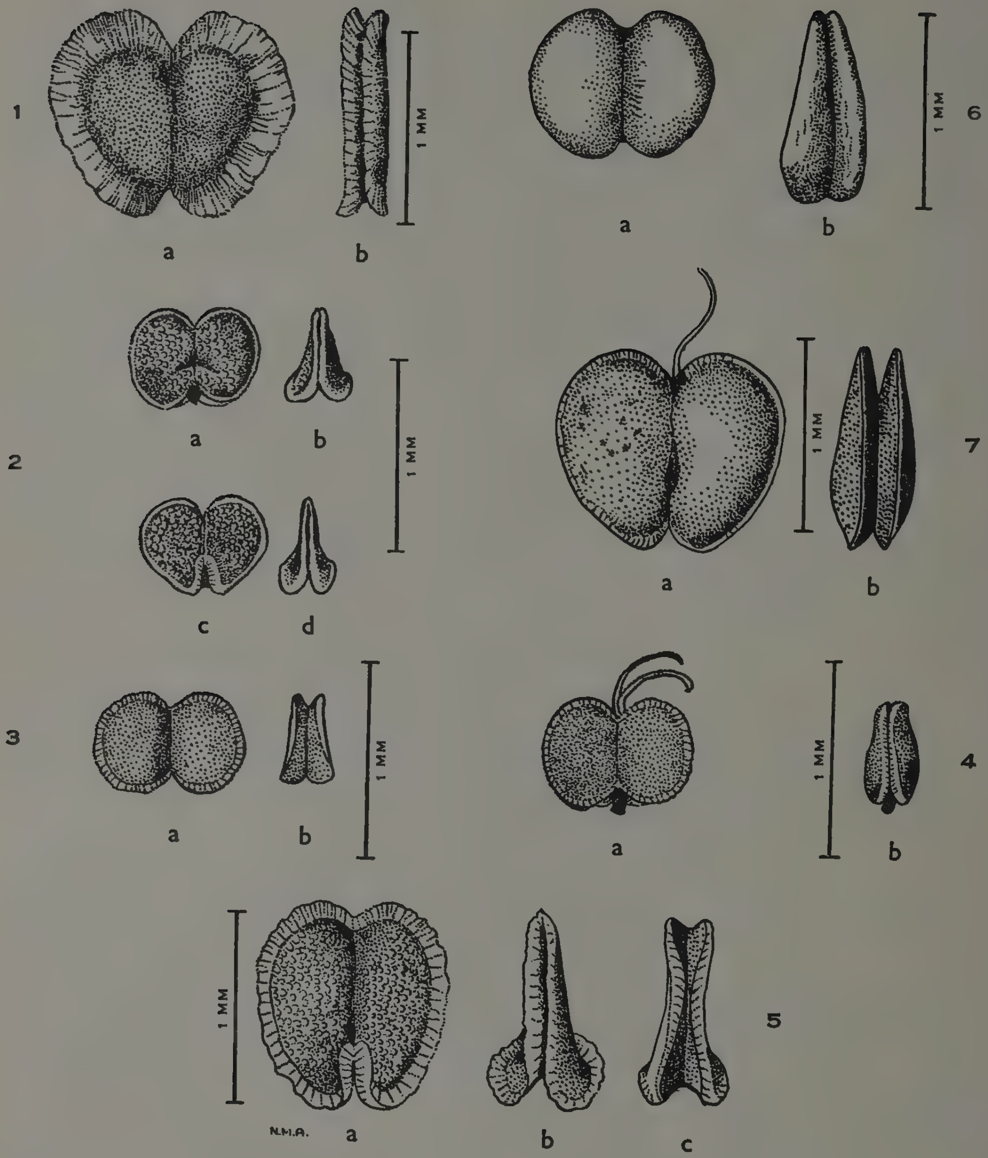

Fig. 1.—*C. muelleri.* *a*, Face of fruit, New South Wales, no collector (NSW 33814). *b*, Edge of fruit, same collection. Fig. 2.—*C. sonderi.* *a*, Face of fruit, L. Cobham, *Bäuerlen.* *b*, Edge of fruit, same collection. *c*, Lower Darling R., *Holding* (MEL). *d*, Edge of fruit, same collection. Fig. 3.—*C. capricorni.* *a*, Face of fruit, Brisbane R., *Bailey* (BRI). *b*, Edge of fruit, same collection. Fig. 4.—*C. brachycarpa.* *a*, Face of fruit, Tasmania, *Archer* (NSW). *b*, Edge of fruit, Apollo B., *Mueller* (MEL). Fig. 5.—*C. umbonata.* *a*, Face of fruit, S. Esk R., *Stuart* (MEL). *b*, Edge of fruit, same collection. *c*, Edge of fruit, Tumbarumba, *Boorman* (NSW). Fig. 6.—*C. antarctica.* *a*, Face of fruit, Campbell I., *Hooker* (MEL). *b*, Edge of fruit, same collection. Fig. 7.—*C. aucklandica.* *a*, Face of fruit, Christchurch ex Auckland Is., *Mason* 3408 (CHR). *b*, Edge of fruit, same collection.

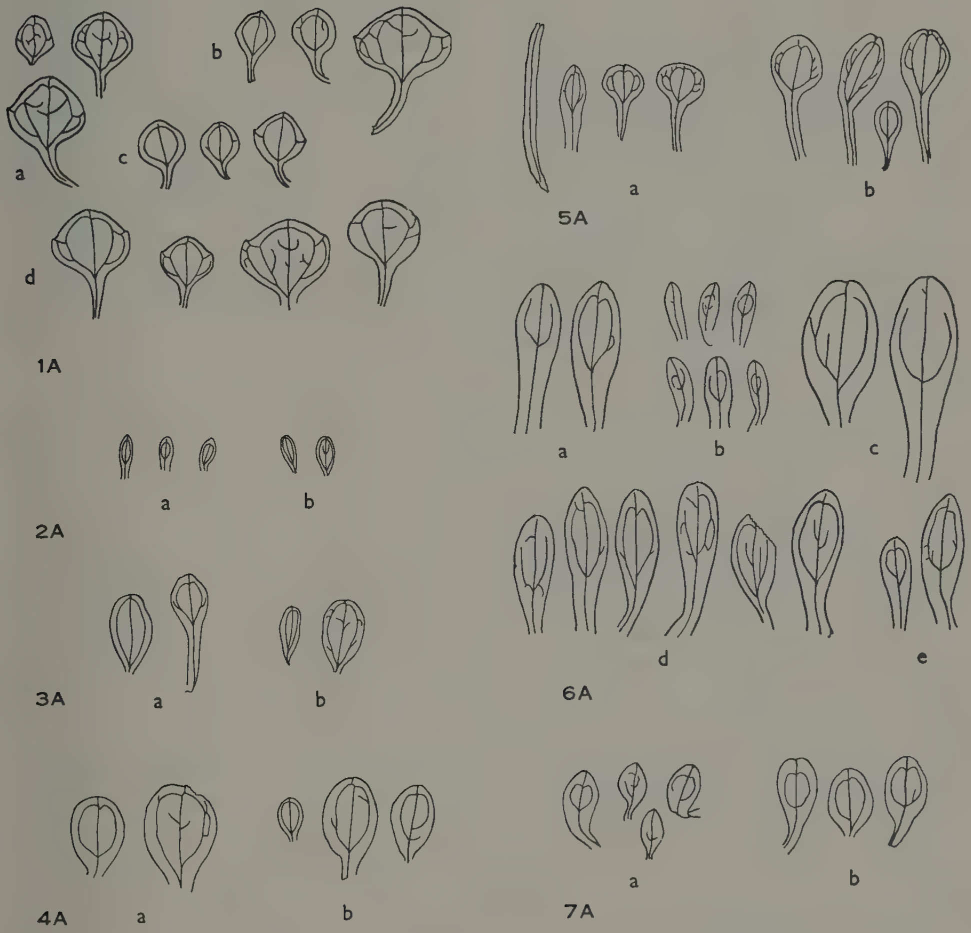

Fig. 1*A*.—*C. muelleri*. Leaves: *a*, Whangaripo Valley, *Petrie* 1920 (WELT); *b*, New South Wales, no collector (NSW 33814); *c*, Parua B., *Petrie* (WELT); *d*, Brisbane R., *Bailey* (BRI 142). Fig. 2*A*.—*C. sonderi*. Leaves: *a*, L. Little Hattah, *Willis* (MEL); *b*, Bundaberg, *Keys* (BRI). Fig. 3*A*.—*C. capricorni*. *a*, Brisbane R., *Bailey* (BRI); *b*, Gracemere, *O'Shanesy* (MEL). Fig. 4*A*.—*C. brachycarpa*. Leaves: *a*, Apollo B., *Mueller* (MEL); *b*, Tasmania, *Archer* (NSW). Fig. 5*A*.—*C. umbonata*. Leaves: *a*, Balcombe R., Black Rock, *Tadgell* (MEL); *b*, Tattiara Country, *Walter* (MEL). Fig. 6*A*.—*C. antarctica*. Leaves: *a*, Campbell I., *Sorensen*, 1943 (CAPE EXPEDN); *b*, Mt. Honey, Campbell I., *Oliver* (CAPE EXPEDN); *c*, Tucker Point, *Findlay* (CAPE EXPEDN); *d*, The Snares, *Kirk* (WELT); *e*, Tucker Cove, *Sorensen* (CAPE EXPEDN). Fig. 7*A*.—*C. aucklandica*. Leaves: *a*, Auckland I., *Hair* (CHR 89341); *b*, Musgrave Peninsula, *Dawbin* (CAPE EXPEDN). Figs. 1*A*–7*A*, all magnifications ×2.

4. **C. brachycarpa** Hegelm., Verh. bot. Ver. Brandenb. **10**: 115–16 (1868).

Figs. 4, 4*A*

Syntypes.—Apollo B., *F. Mueller* (STU); Mt. Disappointment, *F. Mueller* (STU).

Fruit.—Light brown, broader than long (0·8 mm broad by 0·6 mm long to 1·3 mm by 1·0 mm), faces usually slightly convex, evenly winged with a narrow wing; top of mericarps rounded so that there is a fairly broad sinus; commissural groove narrow and shallow. *Flowers.*—Male and female flowers regularly together in the same axil, but only in one axil of a pair of leaves; bracts rare or absent, linear, hyaline, deciduous; styles 1·2–1·5 mm long, erect, persistent; stamens 0·5–2·5 mm long, anthers 0·3–0·5 mm in length and breadth; pollen grains with *c.* 3 "zones of weakness", exine pattern baculate. *Plant.*—Terrestrial, creeping. *Leaves.*—Obovate, 3-nerved, sometimes with free veins from the midrib and free and looped veins from the outer nerves, from 1·6 by 0·7 mm to 7 by 5 mm; peltate hairs present.

General Distribution.—Australia—Victoria and Tasmania.

Specimens Seen

AUSTRALIA—VICTORIA: Tributary of Plenty R. towards Mt. Disappointment, *F. Mueller*, 6.ii.1853 (MEL, isosyntype); Apollo B., *F. Mueller* (MEL, isosyntype). TASMANIA: Gould Country, no collector, Feb. 1877 (NSW); "W. H. Archer's Herbarium of Tasmanian Plants" (NSW).

This species was described as being without bracts by Hegelmaier and they are absent in the Apollo Bay, Plenty River, and Gould Country specimens. The specimen from Archer's herbarium, however, has a few linear, hyaline bracts which fall off readily, though in many quite young flowers there is no sign of them.

If the section *Microcallitriche* is separated from the section *Callitriche*, as by Fassett, *C. brachycarpa* fits into neither. By virtue of its purely terrestrial habit (as evident from the four specimens), its almost uniform leaves, and its fruit being broader than long it should belong to *Microcallitriche*. On the other hand, the abundance of peltate hairs, the long filaments of the stamens, the size of the anthers, and the occasional presence of bracts would put it in the section *Callitriche*.

5. **C. umbonata** Hegelm., Verh. bot. Ver. Brandenb. **9**: 19 (1867).

Figs. 5, 5*A*

Syntypes.—Tasmania, Stuart leg., *c. F. Müller* (STU); in stagnis prope Melbourne Nr. 52, *Dr. Müller* (STU); Darebin Creek, Austr. felix, *Dr. Müller* (STU).

Fruit.—Dark brown, slightly longer than broad, 1 mm broad by 1·1 mm long, inner edges at base of mericarp somewhat swollen and turned outwards, winged all round mericarp including the inner edge at the base, wing pale brown; commissural groove V-shaped, edges parallel. *Flowers.*—Female flowers in both axils of opposite leaves; bracts present; styles about 0·6 mm long, spreading, deciduous; stamens with filaments lengthening to as much as 2·7 mm. *Plant.*—Amphibious. *Leaves.*—Lower leaves linear, sometimes broader at the base than at the top, emarginate, 5–10 mm long, *c.* 0·5 mm wide, rosette leaves more or less orbicular with a broad petiole, 3 to 5-nerved usually with a number of short stumpy free veins on the outside of the outermost nerves.

General Distribution.—Australia—southern New South Wales, Victoria, Tasmania.

Specimens Seen

AUSTRALIA—NEW SOUTH WALES: "Tumberumbah Ck., Tumberumbah", *J. L. Boorman*, Oct. 1916 (NSW); Edward R., no collector, Oct. 1875 (MEL). VICTORIA: Tattiara Country (pastoral country W. of Wimmera District), *C. Walter* (MEL); Goulburn R., *Lewis* (MEL); Mt. Arapiles, *F. M. Reader*, 24.viii.1896 (MEL); near Ararat, *C. Green* (MEL); Balcombe Rd., Black Rock, *A. J. Tadgell*, Oct. 1908 (MEL); Portland, *C. Walter*, Dec. 1898 (NSW); Darebin Ck., *F. Mueller*, *c.* 1852 (MEL, isosyntype); stagnant water on Darebin Ck., *F. Mueller*, Oct. 1852 (MEL, isosyntype). TASMANIA: South Esk R., no collector, Nov., no year (MEL, isosyntype).

Three specimens were referred to by Hegelmaier when describing *C. umbonata*: "1) Tasmania, Stuart leg., *c.* F. Müller; 2) in 'stagnis prope' Melbourne Nr. 52, Dr. Müller; 3) Darebin Creek, Austr. felix, Dr. Müller."

The only Tasmanian specimen in the Hegelmaier Herbarium has a blue label of the type used at an early date by the Melbourne Museum, on which is written by hand only the words "*Callitriche*/South Esk/Tasmania." The only Tasmanian specimen in the Melbourne Herbarium is also from the South Esk River and without a collector's name or date; from the nature of the labels and handwriting it must be of considerable age. As the South Esk River was one of Stuart's collecting places, and as these are the only Tasmanian specimens that are known to have been seen by Mueller and Hegelmaier, there seems no doubt that they are Stuart's.

There is reason to think that the specimens quoted by Hegelmaier under "2)" and "3)" may be in fact from the same collection, but differently labelled. The specimens of the Hegelmaier Herbarium are labelled thus: [*Callitriche umbonata* in stagnis prope Melbourne Dr. F. Müller Ex Herb. Sonder] and [Darebin Creek] (on a blue Melbourne Museum label). In the Melbourne Herbarium itself there is no specimen labelled "in stagnis prope Melbourne" but there is one on which on the sheet itself there is the old type of blue Museum label with [*Callitriche*/Darebin Creek], and on the cover of the sheet [*Callitriche* vernalis/Kuetzing/Stagnant water on the Darebin Creek/October 1852.]. Darebin Creek, a tributary joining the Yarra a few miles from the centre of Melbourne, is now well within the city, but in 1852 could have been described as near Melbourne. The other specimen in the Melbourne Herbarium collected at Darebin Creek has a small newsprint label with [*umbonata*/e Darebin Creek/F.M] stuck to a larger label, which quotes the collection data as given by Hegelmaier for the three specimens, and has a later addition by J. H. Willis to the effect that it is from the herbarium of H. B. Williamson, who received it from the Melbourne Herbarium. It would seem that Mueller collected *Callitriche umbonata* in pools on Darebin Creek near Melbourne in 1852, retained a specimen himself, and distributed one to Sonder as coming from pools near Melbourne and others to Hegelmaier and Williamson as coming from Darebin Creek. Hegelmaier need have had no reason to think that a specimen of Mueller's from "near Melbourne" which he received from Sonder was of the same collection as a specimen from "Darebin Creek" received from Mueller. On the other hand, although the Melbourne Herbarium specimen is dated October 1852, of the second specimen quoted by Hegelmaier he says "Nr. 52",* presumably meaning November 1852. As Mueller did not bother to date some of his specimens at all, it may be supposed that it would not have been important to him to be precise in the matter.

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*This is absent from the label.

There is also in the Hegelmaier Herbarium a specimen of Drummond's from the Swan River identified as *Callitriche umbonata*, with the comment "forma stigmatibus reduxionibus". Should this indeed be *C. umbonata* it extends the distribution of the species some 1500 miles further west than the other most westerly known stations.

6. **C. antarctica** Engelm. ex Hegelm., Verh. bot. Ver. Brandenb. **9**: 20–1 (1867).

Figs. 6, 6*A*

Syntypes.—Antarctic Archipelago, *J. D. Hooker*; Campbell I., *J. D. Hooker*; Kerguelen's Land, *J. D. Hooker.*

Fruit.—Dull brown, about circular (1·1–1·3 mm wide) or broader than long (1·1 mm broad by 0·85 mm long, 1·5 by 1·1 mm), thick, mericarps with slightly convex faces, rounded at the edge, not keeled or winged, commissural groove open and shallow. *Flowers.*—Solitary in one or both of a pair of leaf axils, upper flowers male, lower female; ebracteate or bracts falling early; styles 1·4–3·2 mm long, upright, persistent; stamens with filaments up to 1·3 cm long, thick at the base, tapering to the top; anthers 0·5–1·5 mm wide; pollen grains 27 μ in diam., with 3–6 furrows which are generally long and broad, but sometimes almost circular, exine pattern baculate. *Plants.*—Apparently terrestrial or palustral; stems thick, creeping below with ascending branches 2–10 cm high. *Leaves.*—Spathulate, thick, 3-nerved, sometimes with free veins from the midrib and side nerves, with broad scarious rather noticeably connate base, 2·5–10 mm long, 1·5–4·8 mm wide.

General Distribution.—Subantarctic South America, subantarctic islands, Tasmania (collection of Gunn's *fide* Fassett).

Specimens Seen

KERGUELEN'S LAND: Kerguelen's Land, J. D. Hooker (MEL, isosyntype). THE SNARES: The Snares, *T. Kirk* (AK); the Snares, *B. C. Aston*, Jan. 1909 (AK 5067). CAMPBELL ISLAND: "Campbell's Island", *J. D. Hooker* (MEL, NSW 33828, isosyntypes); pond plant, sea-level, *J. F. Findlay*, Feb. 1945 (CAPE EXPEDN); Campbell I., *Sorensen*, 1943 (CAPE EXPEDN); slopes of Mt. Honey, *R. L. Oliver*, 12.xi.1944 (CAPE EXPEDN); Mt. Lyall, *R. L. Oliver*, 4.xii.1944 (CAPE EXPEDN); maritime rocks, near Tucker Point, *J. F. Findlay* (CAPE EXPEDN); Tucker Cove, *W. B. Brockie*, 23.i.1947 (WELT).

The habit and vegetative characters of *C. antarctica* are quite distinct from all other species of *Callitriche* except *C. aucklandica.* Until the recognition of the fact that plants from the Auckland Islands have distinctly winged fruit with a deep, sharply incised commissural groove, it was reasonable to identify terrestrial plants with thick stems, and thick leaves with broad, membranous, noticeably connate leaf bases, as *C. antarctica.* Some published records are unsupported by fruiting specimens or specimens with ripe pollen and are therefore in doubt.

The species was based on specimens of Hooker's from Antarctic America, Campbell Island, and Kerguelen's Land. Hooker himself (1845: 11–12) considered some of the Campbell Island plants to be identical with those of D'Urville from the Falkland Islands; these he called *C. verna* var. *terrestris.* Presumably, since he referred to Decandolle's "Prodromus" (1820: 70) where there are only four species listed, he associated them with *C. terrestris*, a North American species, the brief description of which could have included *C. antarctica*. (In fact they are not closely related.) His other specimens, including what he saw in the Auckland Islands, he placed simply in *C. verna*. Later Hooker (1879: 20) accepted Hegelmaier's (1864: 54) identification of subantarctic specimens of *Callitriche* as *C. obtusangula* Le Gall, but did not accept *C. antarctica*, already published by Hegelmaier in 1867. He may not have seen Hegelmaier's description of *C. antarctica*, but may have seen only Kidder's (1876: 23) reference to that species. Kidder gave no description and referred only to a manuscript of Engelmann's and Hooker, who referred to Kidder, makes no reference to Hegelmaier's paper of 1867, but mistakenly ascribes Engelmann's description to Hegelmaier's paper of 1864.

The record of *C. antarctica* for the Auckland Islands has rested on the collections made by Kirk,* Tennant, and Laing, and on the assumption that Hooker's record (1845: 11) of *C. verna* L. refers to *C. antarctica* (Cheeseman 1909: 405). Tennant's specimens from Enderby Island do not bear fruit. Laing's and Kirk's specimens do not seem to be in any New Zealand herbarium, though Cheeseman remarked that specimens of the larger form collected by Kirk on the Snares and Auckland Islands bore an abundance of ripe fruit, which had the rounded angles characteristic of the species. However, that *C. antarctica* does occur on the Auckland Islands is established beyond doubt by a specimen of Hooker's at Kew, which according to Dr. R. Melville (personal communication) is conspecific with the Campbell Island syntype.

The specimen from Disappointment Island, Auckland Islands, collected by Turbott (19.xii.1944) is nearer to *C. antarctica* than to *C. aucklandica*, but cannot be placed satisfactorily. The specimen is unfortunately rather scrappy. The fruit has too shallow and narrow a commissural groove for *C. aucklandica*, with no proper wing, though there is something of a border apparent. It is, however, more sharply angled than that of *C. antarctica*. The pollen grains differ from those of *C. antarctica* and *C. aucklandica* in being smaller, 22 μ as against 27 and 25 μ, and in having only three to four furrows against three to six; from *C. aucklandica* it differs in having a baculate exine pattern.

It is with some hesitation that the specimens from the Snares are included here. The fruit viewed face on often shows a very narrow colourless border, but when the epicarp is removed by boiling it is evident that there is no true wing of mesocarp tissue. The commissural groove is rather wider than usual and the top of the mericarps slightly keeled. It is possibly the Snares specimens which prompted Kirk (1899) to refer to the fruit of *C. antarctica* as keeled or slightly keeled. The leaves have a much higher proportion with free veins than those of the Campbell Island material.

Records of *C. antarctica* from Macquarie Island are doubtful. Cheeseman (1919: 24) saw only specimens collected by A. Hamilton and by H. Hamilton which were in young flower only. The specimen in the Melbourne Herbarium collected by

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*Thomas Kirk, who collected on the Snares and Auckland Islands in 1890. H. B. Kirk was on the expedition of 1907 to the subantarctic islands as botanist but visited Campbell Island, not the Auckland Islands. He does not seem to have collected any specimens of *Callitriche*.

Taylor has only one poor, unripe fruit, insufficient for certain identification. There is, however, no sign of a wing and it may indeed be *C. antarctica*.

Three specimens from Heard Island in the Melbourne Herbarium called *C. antarctica* are without flowers or fruit and therefore indeterminable.

Of the *Callitriche* which he referred to as "a very general plant throughout the Antarctic Islands visited by the 'Erebus and Terror' ", Hooker says: "The bracteae, which are caducous, and only exist in the very youngest state of the flower, are singularly falcate, linear-subulate and membranaceous, similar to those of *C. platycarpa* Kützing." No bracts are to be seen on herbarium specimens of *C. antarctica*.

7. C. **aucklandica** sp. nov.

Figs. 7, 7*A*

Holotype.—Auckland I., *J. B. Hair*, Nov. 1954 (CHR 89341).

Herba foliis crassis spatulatis, floribus sine bracteis, fructibus latioribus quam longis (1·2–1·3 mm latis, 1·1 mm longis), alis angustis tenuibus apice saepe latioribus instructis, sinu commissurali alto acuto.

Fruit.—Dark brown, broader than long (1·2–1·3 mm broad by 1·1 mm long), faces rounded, narrowly winged, wing running round the base and top of each mericarp, often broader at the top, membranous; commissural groove fairly wide, deep and sharp. *Flowers.*—Ebracteate, solitary or sometimes 2 of the same sex together; styles erect, persistent, 2–2·5 mm long; stamens with filaments lengthening up to 9 mm, broad and flattened at the base, terete and narrower above; anthers 0·4–0·8 mm broad; pollen grains 25 μ in diameter, with 3–6 large, more or less circular furrows, exine pattern clavate. *Plant.*—With lax upright or more or less sprawling stems, 2–10 cm high, arising from creeping stems. *Leaves.*—Spathulate, thick, 3·7–8 mm long by 1·2–4 mm wide, 3-nerved, occasionally with short free veins, petioles broad and membranous at the base, connate, almost hiding the female flowers.

General Distribution.—Auckland Is.

Specimens Seen

AUCKLAND ISLANDS: French Islet, *J. B. Hair*, Nov. 1954 (CHR); south side Crosier Point, Auckland Islands, *J. B. Hair*, Nov. 1954 (CHR 89342), and also grown in Christchurch—*R. Mason* 3296 (CHR); Auckland Island, *J. B. Hair*, Nov. 1954 (CHR 89341), and also grown in Christchurch from the same plant—*R. Mason* 3290 (CHR), *R. Mason* 3408 (CHR), *R. Mason* 3417 (CHR); Auckland Island, *J. B. Hair*, Nov. 1954 (CHR 89343), and also grown in Christchurch from the same plant—*R. Mason* 3291 (CHR), *R. Mason* 3409 (CHR), *R. Mason* 3297 (CHR); Auckland Island, *J. B. Hair*, Nov. 1954 (CHR 89344), and also grown in Christchurch from the same plant—*R. Mason* 3293 (CHR); in Christchurch from a fifth plant collected on Auckland Island by J. B. Hair, *R. Mason* 3294 (CHR), *R. Mason* 3416 (CHR); grown from a sixth plant collected on Auckland Island by J. B. Hair—*R. Mason* 3289 (CHR), *R. Mason* 3295 (CHR); grown from a seventh plant collected on Auckland Island by J. B. Hair—*R. Mason* 3292 (CHR), *R. Mason* 3415 (CHR); grown from an eighth plant collected on Auckland Island by J. B. Hair—*R. Mason* 3288 (CHR), *R. Mason* 3414 (CHR); grown from a plant collected on Ewing I. by J. B. Hair—*R. Mason* 3299 (CHR); grown from a plant collected on Ocean I. by J. B. Hair—*R. Mason* 3298 (CHR); Musgrave Peninsula, *W. H. Dawbin*, 22.xi.1943 (CAPE EXPEDN); Auckland Island, *E. G. Turbott* (CAPE EXPEDN).

This species strongly resembles *C. antarctica* in vegetative characters. Both have stamens with exceptionally long filaments broader at the base than at the top. The pollen grains of the two species, though differing in ornamentation, shape of aperture, and size, are both much larger than those of other species examined, and are the only two to have three to six furrows. The fruit, however, is winged and has a much more distinct commissural groove than that of *C. antarctica.*

C. aucklandica differs from *C. christensenii* Christophers. of Gough Island in having winged fruit, stamens with much longer filaments, broader at the base than at the top, and not flattened, and in lacking bracts.

C. aucklandica occasionally has two flowers, either both male or both female, in the one leaf axil. In such cases one flower is considerably younger than the other, one anther, for instance, shedding pollen, while the other is just emerging.

C. aucklandica so far as is known is confined to the Auckland Islands. All of the 11 different collections of J. B. Hair from these islands which have fruited are *C. aucklandica.*

All plants were growing terrestrially on peat, either in the open or in the shade of shrubs and tussock.

A plant rooted in soil and placed in a jar of water and kept in a shade house in Christchurch during February and March failed to survive more than 6 weeks; whereas at the same time and in the same conditions plants of *C. petriei* and *C. hamulata*, of terrestrial form and found growing terrestrially, flourished and developed into typical aquatic forms; those of *C. hamulata* flowered and set seed. Attached to the leaves of *C. aucklandica* were large and conspicuous bubbles of gas, but such were not apparent on the other two species. Obviously conditions in the jar would not be exactly those which the plant would meet when growing naturally in water in its native islands, but as there is no definite record of *Callitriche* growing in water on the Auckland Islands, *C. aucklandica* perhaps may not grow as an aquatic.

C. aucklandica is here described as ebracteate, and for all practical purposes it is. On one specimen (CHR 89366), however, two short, linear, membranous bracts, each 0·3 mm long, were seen—a colourless one below a female flower and a brown one below a very young fruit. Both dropped readily. Although very many very young flowers on growing plants were examined there were no other signs of bracts.

8. C. **petriei** sp. nov.

Figs. 8, 8*A* (*a–g*)

Planta vel dioeca vel monoeca foliis tenuibus, spatulatis, floribus sine bracteis, fructibus latioribus quam longis (0·7–1·1 mm latis, 0·6–0·9 mm longis), mericarpellis rotundatis non alatis, sinu commissurali angustato haud profundo.

Fruit.—Greyish brown, broader than long (0·7–1·1 mm broad, 0·6–0·9 mm long), faces strongly convex, thicker at the base than at the top, mericarps rounded, not keeled or winged, commissural groove narrow and shallow. *Flowers.*—Solitary, usually in one leaf axil of a pair of leaves on alternate sides of the stem, without bracts. Styles 1·7–2·2 mm long, erect, more or less persistent; stamens with filaments 2–6 mm long; anthers 0·4 mm long by 0·5 mm broad; pollen grains 20 μ in diameter, with 3(4) indistinct furrows tapering at both ends, exine pattern baculate. *Plant.*—Usually on wet ground, creeping with ascending unbranched stems 3–7 cm high; sometimes submerged, then stems up to 20 cm or more but with no definite rosettes. *Leaves.*—Thin spathulate, obovate to almost orbicular; underwater leaves linear-spathulate or linear and 1-nerved; small, about 2·2 mm long (1·1–8 mm), rounded at the apex, 3-nerved, the larger leaves often with short, sometimes branched side veins.

8(*a*). C. **petriei** subsp. **petriei**

Holotype.—Ngaruawahia, Waikato R., *D. Petrie*, 4.ii.1906 (WELT).

Dioeca, foliis 1·1–5 mm longis, fructibus 0·7–0·9 mm latis, 0·6–0·7 mm longis.

General Distribution.—New Zealand—North Island south of Auckland Isthmus, South Island.

Specimens Seen

New Zealand—north island: *J. Buchanan* (MEL); Hunua Falls, Wairoa South, Auckland, *D. Petrie*, Feb. 1902 (WELT); Ngaruawahia, *D. Petrie*, 4.ii.1906 (WELT); Rotoaira, *S. Berggren*, Jan. 1875 (WELT); Rotoaira, no collector or date, possibly part of Berggren's specimen (WELT); Kaitoke L., S. of Wanganui, *R. Mason* 4155 (CHR); Pauri L., S. of Wanganui, *R. Mason* 4134 (CHR); Roto Kawau, N. of Wangaehu, *R. Mason* 4126 (CHR); Roto Kawau, N. of Wangaehu, *R. Mason* 4125 (CHR); L. Alice, near Bulls, *R. Mason* 4090 (CHR); Oro Bush, *H. Tryon* (BRI); Hamilton's Bend, Manawatu District, *R. Mason*, 11.iii.1948 (CHR); Manawatu R. at Foxton, *H. H. Allan* (CHR); Lakeside Reserve, L. Wairarapa, *R. Mason* 1372 (CHR). south island: N. end of Whanganui Inlet, *R. Mason and N. T. Moar* 4877 (CHR); L. Rotoiti, *R. Mason and N. T. Moar* 5027 (CHR); Tuamarina Swamp, Marlborough, *R. Mason* 3067 (CHR); near Tuamarina, *R. Mason* 3056 (CHR); drain near lower Wairau R., Marlborough, *R. Mason* 3087 (CHR); Blenheim, *R. Mason* 913 (CHR); Gooseberry Gully, Molesworth, *L. B. Moore*, 26.i.1952 (CHR); Tidal Ck. at bridge on Carter's Beach Rd., Buller Co., *R. Mason and N. T. Moar* 1673 (CHR); near Westport, seaward of Carter's Beach Rd., *R. Mason and N. T. Moar* 1708 (CHR); Westport, *R. Mason and N. T. Moar* 2350 (CHR); Greymouth, *R. Helms* (BRI, MEL); L. Grassmere, Canterbury, *R. Mason* 706 (CHR); SE. of L. Georgina, *R. Mason and N. T. Moar* 4474 (CHR); N. side of Rakaia R. mouth, *R. Mason* 3274 (CHR); Eastern Otago, *D. Petrie* (WELT)—mixed with *C. stagnalis*; Beaumont, Clutha R., Tuapeka Co., *D. Petrie*, Oct. 1890 (WELT); Dunedin, *B. C. Aston*, 1894 (WELT); Green I., Otago, *D. Petrie* (WELT); near Dunedin, G. M. Thomson Herbarium, Jan. 1880 (BRI); L. Tuakitoko, *R. Mason and N. T. Moar* 969 (CHR); Port Molyneux, *R. Mason and N. T. Moar* 1018 (CHR); Kelso, near Tapanui, Otago, *D. Petrie*, Feb. 1891 (WELT); Ryal Bush, Southland, *T. Kirk* (WELT); Winton Bush, Southland, *T. Kirk*, 8.xii.1883 (WELT); L. Katherine, *R. Mason*, 21.iv.1949 (CHR 65452, CHR 65453); head of L. Duncan, Fiordland, *W. R. Philipson* 148 (CHR); Waituna lagoon, Southland, *R. Mason and N. T. Moar* 1219 (CHR).

C. petriei subsp. *petriei* differs from all other members of the genus in being dioecious. The one-nerved linear leaves are not common. They have only been found once, on a plant in a small lake with particularly clear water south-east of Lake Georgina, in the eastern foothills of the Southern Alps. The topmost leaves of these plants, though some inches below the surface, were spathulate or obovate. Plants transplanted to a jar of water and grown in Christchurch developed an abundance of obovate three-nerved leaves, some with free veins.

C. petriei subsp. *petriei* appears to be what Kirk chiefly had in mind when he recorded "*C. Muelleri* Sond. var. *C. obtusangula* Le Gall. ex Hegelm." for New

Zealand (1899: 156). A specimen collected at Lake Rotoaira by Berggren in January 1875,* and now in the Dominion Museum, has the original determination "*C. obtusangula*", and Kirk has inserted the word "*Muelleri*" before "*obtusangula*". What seems to be a selection from this is labelled in Kirk's writing: [*Callitriche Muelleri* Sonder v. *obtusangula*/T. Kirk Stud. Fl. N.Z./*C. obtusangula*, Le Gall. ex Hegel. Monogr./Callitri. 54/ Roto Aira.].

Kirk, however, determined a collection of his own from Waipipi Road, near Invercargill, as *C. muelleri* var. *obtusangula* though it has typical *C. stagnalis* fruit; and on another specimen of his own from the Bay of Islands, which has typical *C. muelleri* fruit with the extremely broad wing, he has the note: "a form with a narrow wing". Kirk seems to have been altogether confused. His description of "*C. muelleri* v. *obtusangula*" states that the fruit has a very narrow wing, which fits neither *C. obtusangula* Le Gall ex Hegelm. nor the specimen of Berggren which Kirk apparently took as his standard.

Apart from being dioecious, *C. petriei* subsp. *petriei* differs from *C. obtusangula* in lacking bracts and in having smaller fruit (less than 1 mm in diameter as against 1·5–2 mm), which are broader than long, not longer than broad as in *C. obtusangula*. It is not closely allied to *C. muelleri*; nor for that matter is *C. obtusangula*.

8(*b*). **C. petriei** subsp. **chathamensis** subsp. nov.

Fig. 8*A* (*h*)

Holotype.—Tupuangi Lagoon, Pitt I., Chatham Is., *B. G. Hamlin* 692 (WELT).

Monoeca, foliis 2·5–8 mm longis, fructibus 0·7–1·1 mm latis, 0·6–0·9 mm longis.

General Distribution.—Chatham Is.

Specimens Seen

CHATHAM ISLANDS: Chatham Islands, *H. H. Travers*, 1872 (MEL); Waitangi, *L. Cockayne and F. D. Cox* 1480 (WELT, AK); L. Huro, Chatham Island, *B. G. Hamlin* 659 (WELT); Tupuangi Lagoon, Pitt I., *B. G. Hamlin* 692 (WELT).

The pollen grains from the Pitt Island specimen are similar to those of *C. petriei* subsp. *petriei*, except that they average 19 μ as against 20 μ. This cannot be taken as significant, as the material was poor.

C. petriei, when not in flower or fruit, can usually be distinguished from *C. stagnalis* by its smaller and much more delicate leaves and by the different pattern of venation; many of the specimens listed were identified by leaf characters alone.

C. petriei in many respects resembles *C. brachycarpa*. The fruit are similar in that they are broader than tall, emarginate, with convex faces, and an extremely

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*In the Dominion Museum herbarium there are two specimens of *Callitriche* collected in New Zealand by Berggren—one from the Bay of Islands originally determined as *C. macropteryx*, one from Rotoaira originally determined as *C. obtusangula*. In the Kirk Herbarium in the Dominion Museum there are two specimens which match these, without collector's name or dates, but one from the Bay of Islands and one from Rotoaira, with full synonymies in Kirk's handwriting, both in packets of a type of lined writing paper not used by Kirk for any other of his *Callitriche* specimens. It seems probable that the specimens in the Kirk Herbarium were selected from Berggren's by Kirk for use as standard reference material.

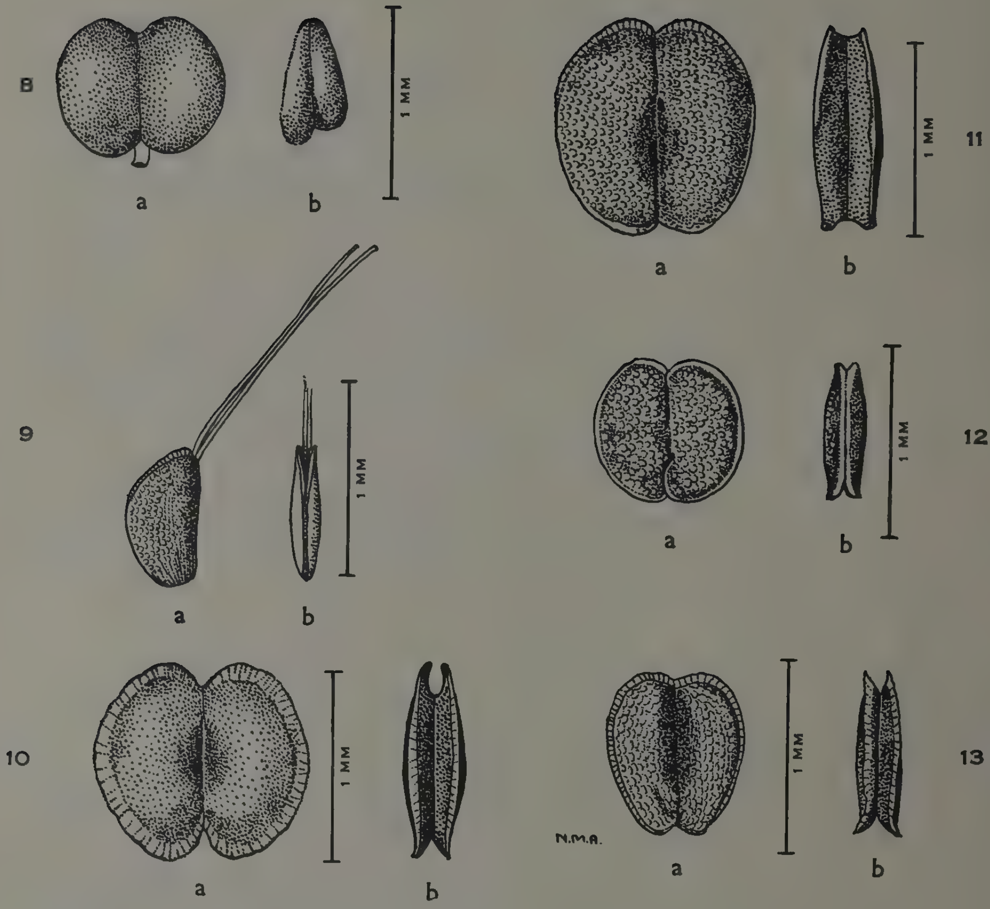
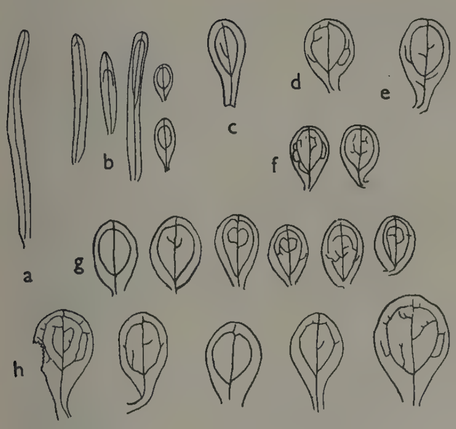
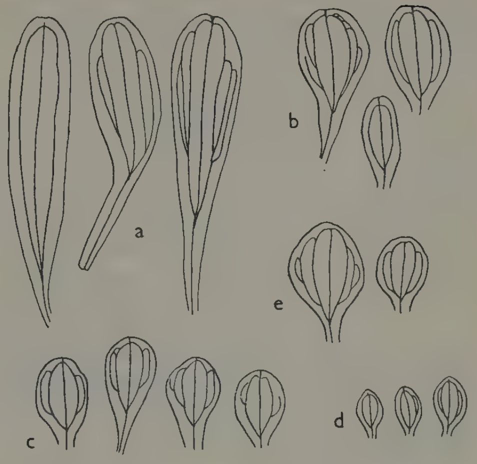


Fig. 8.—*C. petriei*. *a*, Face of fruit, Ngaruawahia, *Petrie* (WELT). *b*, Edge of fruit, same collection. Fig. 9.—*C. heterophylla*. *a*, Face of fruit, Waikato R., *Cheeseman* (CANTY). *b*, Edge of fruit, same collection. Fig. 10.—*C. stagnalis*. *a*, Face of fruit, L. Grassmere, *Mason* 705 (CHR). *b*, Edge of fruit, same collection. Fig. 11.—*C. hamulata*. *a*, Face of fruit, L. Elterwater, *Mason* 3160 (CHR). *b*, Edge of fruit, same collection. Fig. 12.—*C. cyclocarpa*. *a*, Face of fruit, Yarra Yarra, *Mueller* (MEL). *b*, Edge of fruit, same collection. Fig. 13.—*C. palustris*. *a*, Face of fruit, Broken R., *Say* (MEL). *b*, Edge of fruit, same collection.



8A



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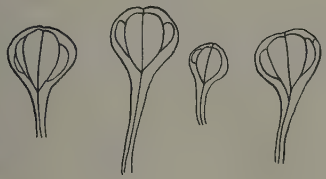
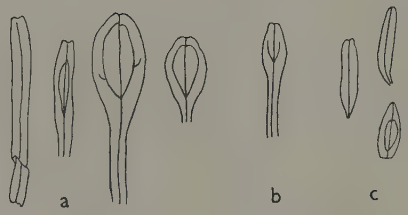
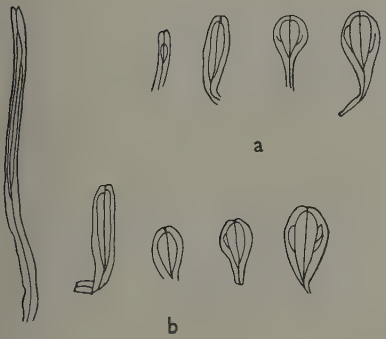


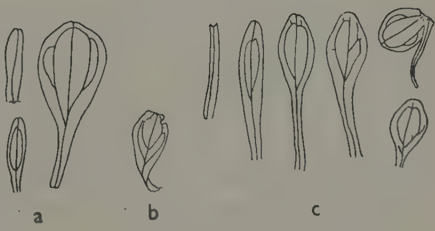
9A



11A



13A



12A

Fig. 8*A*.—*C. petriei*. Leaves: *a*, Near L. Georgina, *Mason and Moar* 4474 (CHR); *b*, Waituna Lagoon, *Mason and Moar* 1219 (CHR); *c*, L. Katherine, *Mason* (CHR 65453); *d*, Westport, *Mason and Moar* 1708 (CHR); *e*, Blenheim, *Mason* 913 (CHR); *f*, Carter's Beach Rd., *Mason and Moar* 1673 (CHR); *g*, Ngaruawahia, *Petrie* (WELT); *C. petriei* subsp. *chathamensis*: *h*, Chatham Is., *Travers* (MEL). Fig. 9*A*.—*C. heterophylla*. Leaves: Waikato R., *Cheeseman* (CANTY). Fig. 10*A*.—*C. stagnalis*. Leaves: *a*, Kaihu R., *Mason and Moar* 28 (CHR), submerged leaves; *b*, Monoweit, *Sutton* (MEL); *c*, Linton, *Williamson* (MEL); *d*, Tauwharenikau, *Zotov* (CHR); *e*, Mt. St. John, *Petrie*, 1890 (WELT), rosette leaves. Fig. 11*A*.—*C. hamulata*. Leaves: *a*, Ex L. Elterwater, and grown submerged at Christchurch, *Mason* 3160 (CHR); *b*, L. Jasper, *Mason* 3162 (CHR); *c*, Linton, *A.J.E.* (MEL). Fig. 12*A*.—*C. cyclocarpa*. Leaves: *a*, Hawkesdale, *Williamson* (BRI); *b*, Yarra Yarra, *Mueller* (MEL); *c*, Swan Hill, *Luehmann* (MEL). Fig. 13*A*.—*C. palustris*. Leaves: *a*, Goulburn R., *Say* (MEL); *b*, Broken R., *Say* (MEL). Figs. 8*A*–13*A*, all magnifications ×2.

narrow and shallow commissural groove. Both have persistent styles, strict when young. The subaerial leaves are similar in shape and have the same type of venation. The fruit of *C. petriei*, however, is usually smaller than that of *C. brachycarpa*, not such a bright brown, entirely without wing or keel, with faces more strongly convex, and with a much less noticeable cell pattern. In *C. petriei* there are as many as 44–52 cells per millimetre in the endocarp, against only about 24 in *C. brachycarpa*. Whereas the male and female flowers in *C. brachycarpa* occur regularly together in only one axil of a pair of leaves, *C. petriei* is either dioecious or has only one flower in one or both the axils of a pair of leaves. Both species have baculate pollen grains, though so far as evidence is available those of *C. petriei* differ from those of *C. brachycarpa* in having furrows, as against zones of weakness. *C. petriei* is amphibious, *C. brachycarpa*, so far as is known, terrestrial.

The fruit of *C. petriei*, though smaller and broader in proportion, is somewhat similar to that of *C. antarctica*, but the plants differ in other respects; in particular the thin delicate leaves of *C. petriei* contrast strongly with the large thick leaves of *C. antarctica*.

9. **C. heterophylla** Pursh emend. Darby var. **heterophylla.**

Figs. 9, 9*A*

C. heterophylla Pursh, Fl. Amer. Sept. **1**: 3 (1814), *nomen ambiguum*; Darby, Bot. Southern States, 311 (1841).

Fruit.—Brown, about as long as broad or very slightly longer (0·6–1·0 mm, but usually 0·7–0·8 mm), slightly heart-shaped in outline; mericarps with convex faces, wingless or sometimes with a narrow brown wing at the top; commissural groove very shallow and narrow. *Flowers.*—Male and female flowers together in both axils of each pair of leaves; bracts white and conspicuous, more or less persistent; styles 1–6 mm long, erect or spreading, persistent or caducous; stamens with filaments up to 4 mm long; anthers 0·25 mm long, 0·3 mm or more broad; pollen grains 16 μ in diameter, 3 "zones of weakness", exine pattern verrucate. *Plant.*—Aquatic, tall, ascending, little branched, often with floating rosettes. *Leaves.*—Very variable, often linear, shallowly bidentate, 1-nerved at the lower nodes with a rosette of floating obovate leaves, or all linear, or all obovate, or oblong on plants stranded on the mud; obovate leaves 3- to 7-nerved.

General Distribution.—North America, two records from South America.

Specimens Seen

New Zealand—north island: Waikato R., *T. F. Cheeseman*, April 1900 (CANTY 851/4).

The one New Zealand specimen has a few 1-nerved and elliptic-linear leaves, but most of the leaves are 3- to 7-nerved, blunt, broad, suddenly narrowed and tapering to the base, matching those in Fassett's (1951) illustration (Plate 1168, Fig. 4). For the most part the mericarps on one side of the fruit only have been developed. This does not seem to be of any special significance, as undeveloped mericarps occur occasionally in all other species in New Zealand. Most of the fruits have the small wing that is sometimes present.

As only two collections of *Callitriche* have come from the Waikato River since this specimen, there is nothing to indicate that this species has become established.

10. **C. stagnalis** Scop., Fl. Carn., 2nd Ed., 251 (1772).

Figs. 10, 10*A*

Fruit.—Very short-stalked, pale, more or less round, 1·2–1·7 mm broad, faces more or less flat, winged; wing broad, running round the base and usually also the top of the mericarp; mericarps semicircular, or semilunar; facial groove short, deep, and often wide; commissural groove wide, tapering towards the top, deep, somewhat rounded. *Flowers.*—Male and female flowers solitary or the two occurring together in the leaf axils; bracts white, falcate, persistent; styles up to 2·5–3·5 mm long, erect recurved in fruit, persistent; stamens with filaments about 2 mm long; anthers about 0·2 mm in length and breadth; pollen grains 17 μ in diameter, *c.* 3 "zones of weakness", exine pattern baculate. *Plant.*—Amphibious, variable, up to 3 ft tall in water, or creeping subaerially on mud and forming a turf. *Leaves.*—Variable, linear-spathulate, spathulate, obovate or ±rounded or slightly emarginate (never linear), 3-, 5-, or 7-nerved, the uppermost forming well-marked rosettes, submerged leaves being narrower in proportion than subaerial and floating leaves; size from 2·5 mm long by 1 mm broad (terrestrial) to 25 by 6 mm (submerged), average *c.* 7 by 6 mm.

General Distribution.—North America (probably introduced), Europe, Asia, Australia, New Caledonia, New Zealand.

Specimens Seen

AUSTRALIA—NEW SOUTH WALES: N.S.W., *J. J. Fletcher*, 27.x.1889 (NSW); near Sydney, *E. Betche*, Oct. 1881 (NSW); Birrong, *L. A. S. Johnson*, 20.viii.1946 (NSW); Kogarah, *J. H. Camfield*, 1.i.1900 (NSW); Kogarah, *J. H. Camfield*, Oct. 1900 (NSW); Alexandria Swamp, *J. J. Fletcher*, 27.x.1888 (NSW); Mt. Wilson, *A. G. Hamilton*, Dec. 1898 (NSW); Murray's Crossing, Tumbarumba, *E. G. McBarron*, 2.i.1948 (NSW). VICTORIA: Linton, *H. B. Williamson*, 1913 (BRI); McVeigh's, Upper Yarra R., *A. J. Tadgell*, Jan. 1910 (MEL); Narracan Ck., near Moe, *P.R.H. St. J.*, 11.iii.1929 (MEL); Rosstown, no collector, 20.xi.1902 (MEL); Kilmore, *A. Meebold* 21524 (NSW); Cheltenham-Sandringham area, *A. J. Tadgell*, Oct. 1909 (MEL); Cheltenham, *Louie Roberts*, 1910 (MEL); Pakenham, *P.R.H. St. John*, 26.xi.1904 (MEL); Monoweit, *C. S. Sutton*, Nov. 1904 (MEL). SOUTH AUSTRALIA: Humbug Scrub, *Miss Eardley*, 11.x.1931 (AD); Kersbrook, *C. M. Eardley*, 11.x.1939 (AD); Carey's Gully, near Adelaide, *J. B. Cleland*, 18.xi.1944 (AD); Beaumont, near Adelaide, *J. B. Cleland*, Oct. 1933 (AD); Mt. Lofty Ra., SSE. of Adelaide, weir of Onkaparinga R., *Hj. Eichler* 12266 (AD); Stirling West, near Mt. Lofty, *E. H. Ising*, 1.i.1957 (AD 95708087, 95708088); Kadlunga, no collector, 1882 (AD). WESTERN AUSTRALIA: Harvey, *G. R. W. Meadly*, 26.xi.1951 (PERTH); Manjimup, *R. D. Royce* 2982 (PERTH).

NEW ZEALAND—NORTH ISLAND: Hukatere, North Cape Peninsula, *H. Carse*, Jan. 1913 (CANTY); Maitai B., Rangia-whia Peninsula, *R. Cooper*, 4.xii.1949 (CHR 81880, 81881); Kaitaia, *H. Carse*, 14.viii.1918 (CANTY); Taipa Beach, *R. Cooper*, 11.i.1950 (AK); Oruru Stream, near Taipa, *R. Cooper*, 10.i.1950 (AK); Kaeo, *R. Mason and N. T. Moar* 340 (CHR); Awanui, *H. Carse*, Feb. 1910 (AK); Bonnetts' Road, Kaitaia, *R. Mason and N. T. Moar* 257 (CHR); L. Tongonge, *R. Mason, N. T. Moar, and R. Cooper*, 29.xi.1949 (AK); drainage channel, L. Tongonge, *R. Mason, N. T. Moar, and R. Cooper*, 29.xi.1949 (AK); L. Tongonge, *R. Mason and N. T. Moar* 256 (CHR); Waitangi Falls, Bay of Islands, *D. Petrie*, March 1920 (WELT); S. of Mitimiti, Mangonui Co., *R. Cooper*, 26.xi.1949 (AK 35680); S. of Mitimiti, *R. Cooper*, 26.xi.1949 (AK 35685);

Waihopai Stream, S. of Mitimiti, *R. Mason and N. T. Moar* 166 (CHR); Waihopai Stream, *R. Mason and N. T. Moar* 173 (CHR); E. of Opononi, *R. Mason and N. T. Moar* 136 (CHR, AK); Kaihu R., *R. Mason and N. T. Moar* 85 (CHR); Maitahi, Kaihu R., *R. Mason and N. T. Moar* 28 (CHR); Dargaville-Kaihu Rd., *R. Cooper*, 23.xi.1949 (AK); Otekairangi, *R. Mason and N. T. Moar* 394 (CHR); Otekairangi, *R. Mason, N. T. Moar, and R. Cooper* (AK 35877, 35889); Medland's Beach, Great Barrier I., *R. Mason* 448 (CHR); Avondale South, near Auckland, *H. Carse*, 24.x.1922 (CANTY); Epsom, Auckland, *D. Petrie*, 1889 (WELT); Mt. Hobson, Auckland, *D. Petrie*, Oct. 1918 (WELT); lagoon on Mt. St. John, Auckland, *D. Petrie*, Oct. 1890 (WELT); lagoon on Mt. St. John, *D. Petrie*, Dec. 1914 (WELT, NSW); St. John's L., Auckland, *L. M. Cranwell*, 14.vi.1930 (AK); L. St. John, *D. Petrie*, mid Nov. 1911 (NSW); Thompson's L., Waiuku, *N. T. Moar* 482 (CHR); Tauhei, Piako Co., *H. Carse*, Nov. 1923 (CANTY); Waikato R., *H. Carse*, Sept. 1899 (CANTY); Waikato R., near Churchill, *T. Kirk* (WELT); Waikato R., *T. F. Cheeseman* (AK); Maungatautari Mt., near Cambridge, *J. E. Attwood*, 1932 (AK); Te Aroha, *H. B. Matthews and H. Carse*, 30.xii.1915 (CANTY); Dunphail, Te Akatea, Raglan Co., *D. Petrie*, 16.i.1921 (WELT); Tokaanu Stream, L. Taupo, *G. E. Gubb*, 16.vii.1941 (WELT); Holly Flat Swamp, Mt. Egmont, *B. G. Hamlin* 412 (WELT); Douglas, Taranaki, *R. Mason* 4252 (CHR); Hautapu R., SW. Kaimanawas, *A. P. Druce* D.E.G. 836, May 1950 (CHR); Pipiriki, Wanganui R., *D. Petrie*, Feb. 1923 (WELT); Pauri L., S. of Wanganui, *R. Mason* 4138 (CHR); L. Alice, near Bulls, *R. Mason* 4089 (CHR); Omanuka Lagoon, S. of Rangitikei R., *R. Mason* 4059 (CHR); Pohangina, *N. T. Moar* 2545 (CHR); Bunnythorpe, *V. D. Zotov*, 19.xii.1928 (CHR); L. Huniu, Himitangi, *N. T. Moar*, 23.viii.1948 (CHR); Paiaka, *A. J. Healy*, Dec. 1942 (CHR); Moutoa Estate, *N. T. Moar*, 8.xi.1950 (CHR 61149, CHR 61148, CHR 61147); Waitarere, *R. Mason* 4025 (CHR); E. of Mt. Arawaru, Tararuas, *V. D. Zotov*, 6.iii.1932 (CHR); Otaki, *H. H. Allan*, 28.xii.1940 (CHR); Waikanae, *R. Mason* 2892 (CHR); Paraparaumu, *H. H. Allan*, 8.xii.1940 (CHR); Tauherinikau Valley, *R. Mason* 8.ii.1942 (CHR); Tauwharenikau [Tauherinikau], *V. D. Zotov*, 17.i.1947 (CHR); Mangaroa Swamp, *V. D. Zotov*, 30.xi.1944 (CHR); Mangaroa Valley, no collector, 15.v.1955 (CHR); L. Wairarapa, *R. Mason* 758 (CHR); Orongorongo R., *R. D. Scott*, Oct. 1933 (WELT); Wainui-o-mata Dam, *L. B. Moore*, 16.i.1939 (CHR); S. of Wainui-o-mata township, *A. J. Healy* 50/329 (CHR); Gollans Valley, Wellington, *R. Mason*, 15.iv.1948 (CHR); L. Kohangapiripiri, *R. Mason*, 29.v.1949 (CHR); Black Bridge, near Wadestown, Wellington, *R. Mason* 618 (CHR); Kelburn, Wellington, *H. H. Allan*, Oct. 1938 (CHR); Ohariu Valley, *R. Mason*, 26.ix.1948 (CHR); C. Palliser, *L. B. Moore*, 6.iii.1954 (CHR). SOUTH ISLAND: Maungarakau Swamp, Nelson, *R. Mason and N. T. Moar* 4822 (CHR); W. of Wakefield, Nelson, *R. Mason and N. T. Moar* 4626 (CHR); Pelorus R., *R. Mason and N. T. Moar* 4581 (CHR); Tuamarina Swamp, *R. Mason* 3071 (CHR); C. Foulwind, *D. Petrie*, 4.ii.1913 (WELT); Fairdown, Buller Co., *R. Mason and N. T. Moar* 1943 (CHR); Fairdown, *R. Mason and N. T. Moar* 2042 (CHR); Slab Hut Ck., near Tawhai, Inangahua Co., *C. M. Smith*, 8.x.1956 (CHR); Leithfield, North Canterbury, *A. J. Healy* 54/542 (CHR); Ashley Gorge, *N. T. Moar* 2543 (CHR); near Cust, *R. Mason* 3229 (CHR); Bridlepath, near Lyttleton, *J. B. Armstrong*, 26.ix.1921 (CANTY); L. Sarah, Cass, *W. R. Philipson*, May 1955 (CHR); L. Grassmere, Canterbury, *R. Mason* 705 (CHR); Ashburton, *H. H. Allan*, Dec. 1919 (CHR); Fairlie, *D. Petrie* (CANTY); Fairlie, *D. Petrie*, 8.ii.1911 (WELT); N. of Lindis Pass, *I. McNeur*, 3.x.1949 (CHR); Middlemarch, Strath Taieri, *A. Wall* (WELT); Eastern Otago, *D. Petrie* (WELT)—mixed with *C. petriei*; Beaumont, Clutha R., *D. Petrie* (WELT); Double Hill, Otago, *R. Mason* 851 (CHR); Signal Hill, Dunedin, *B. C. Aston* (WELT—T. Kirk's private collection and McMahon collection); Signal Hill, Dunedin, *D. Petrie*, 2.xii.1912 (WELT); L. Waihola, *R. Mason and N. T. Moar* 940 (CHR); Kelso, near Tapanui, *D. Petrie*, Feb. 1891 (WELT); Waipipi Rd., near Invercargill, *T. Kirk*, 10.ii.1890 (WELT).

C. stagnalis is perhaps the tallest and most robust species of *Callitriche*. Its pale, broadly winged fruit are distinct, but even when not fertile it can often be readily distinguished from other species in Australia or New Zealand by its size, the almost orbicular-rosette leaves, the lack of linear underwater leaves, and by the venation. Smaller plants, especially those growing out of water on mud—a condition in which the full typical venation is less likely to be developed—cannot so often be determined when not in flower or fruit.

As understood by most authors *C. stagnalis* includes Kuetzing's *C. platycarpa*. Schotsman (1954), who maintains *C. platycarpa*, points out that its carpels are less divergent than those of *C. stagnalis*, the stigmas less spreading, and that *C. platycarpa* has linear stem leaves, whereas *C. stagnalis* never shows such leaves. He gives a diploid number of 20 for *C. platycarpa* and one of 10 for *C. stagnalis*. Dr. J. B. Hair (personal communication) has found a chromosome count of $2n = 10$ for New Zealand plants. There is no reason to suppose that *C. platycarpa* occurs in Australia or New Zealand.

This is the most common amphibious *Callitriche* in New Zealand and, so far as is known, the amphibious species most widespread in Australia. It has hitherto in New Zealand literature generally been referred to *C. verna*. Hooker in the additions to the Handbook placed the "*C. verna*" of New Zealand in *C. stagnalis* Scop. on account of the broad wings of the fruit. This was not overlooked by Kirk, as shown by the synonyms cited by him under *C. muelleri* on labels in his herbarium. However, Kirk understood Hooker to mean (as perhaps he did) that the comparatively narrowly winged *Callitriche* in New Zealand with which he was acquainted was *C. verna* and the most broadly winged one was *C. stagnalis*, which he therefore treated as a synonym of *C. muelleri*. Colenso (1888: 190–1) had also evidently noticed Hooker's reference to *C. stagnalis*, but later writers do not mention it.

Australian specimens have likewise for the most part been attributed to *C. verna*, although Eardley and Meebold had recognized their collections as *C. stagnalis* and Black recorded it as the one species occurring in South Australia, though he later changed his mind. Curtis (1956: 192) records it as the species present in Tasmania.

The venation in Australian specimens tends to be more irregular than in the New Zealand ones. Instead of one looped outer nerve, there are two or three loops one above the other, or a loop is not quite completed. These irregularities do not obscure the basic pattern and do not occur often on one plant.

11. C. **hamulata** Ktzg. in Koch, Syn. Flor. Germ. et Helv., 1st Ed. (1837).

Figs. 11, 11*A*

Fruit.—Usually sessile but occasionally with conspicuous peduncles, dark brown, nearly circular, or slightly longer than broad (1·2–1·4 mm), faces of mericarps flat, thickest in the middle, with a very narrow, often white wing, often slightly broader at the top, which runs right round the top of the mericarp and often right round the base, commissural groove wide, shallow, and often flat. *Flowers.*—Male and female flowers occurring singly in the axils of the stem and lower rosette leaves, submerged, bracts absent or rarely present; styles deflexed close to the fruit, 1·2 mm long or more, usually deciduous but the base often remaining; stamen *c.* 1 mm long, anther 0·5 mm in length and width. *Plants.*—Amphibious; aquatic form with tall branched stems bearing floating rosettes and linear underwater leaves; land form creeping with ascendant branches. *Leaves.*—Submerged leaves linear, 1-nerved, somewhat wider at the tip, deeply bidentate, 6 mm–3 cm long, 0·5–1 mm wide; rosette leaves spathulate, 3-nerved with occasionally a small free vein on the outside of the 2 outer nerves; leaves of land form linear-elliptic to elliptic, 1(–3)-nerved.

General Distribution.—Greenland, Europe, Australia, New Zealand.

Specimens Seen

AUSTRALIA—VICTORIA: Linton, *A.J.E.* in Herb. H. B. Williamson (MEL).

NEW ZEALAND—SOUTH ISLAND: L. Jasper, Awatere Valley, Marlborough, *R. Mason* 3162 (CHR); L. Elterwater, Marlborough, *R. Mason* 3160 (CHR).

In the specimen from Linton, Vic., the fruits have conspicuous peduncles, some as long as 15 mm. According to Schotsman (1954: 328, 362) the land form of *C. hamulata* sometimes has stalked fruit. Apparently, stalked fruit may occur in water forms also, for the Linton specimen has every appearance of being such, and is described on the label as a "water plant". The specimen is only a scrap, and the fruit on the small side, 0·9 mm in diameter, but the few mature fruits have the characteristics of *C. hamulata*, and bracts are lacking.

The ripe fruit on the New Zealand specimens are somewhat darker (almost black), and have a much more colourless wing than most of the fruit on specimens from Europe which I have seen. They agree in all essentials, however, and there are a few European fruits which the New Zealand fruits match almost exactly.

The specimen from Lake Jasper is a land form which was growing on mud and has only a few poorly developed fruit. When portions of it were grown in a jar of water they developed into the typical water form and bore typical mature fruit. Conversely, seeds from Lake Elterwater grown in pots developed into land plants similar to those from Lake Jasper.

The longest linear leaves on the Australian and New Zealand specimens are no more than a third as long as the longest on European specimens, nor do they have the bidentate teeth so well developed, nor the typical swollen tip; but they match the leaves of some European specimens quite well.

12. C. **cyclocarpa** Hegelm., Verh. bot. Ver. Brandenb. **10**: 116 (1868).

Figs. 12, 12*A*

Type.—Yarra Yarra, *F. Mueller* (STU).

Fruit.—Dark brown, more or less circular, 0·8–0·85 mm in diameter, bases of mericarps at inner edge pushing against each other, or sometimes overlapping so that the fruit is thicker at the middle of the base than at the top but not strumose, keeled or slightly winged; commissural groove V-shaped, sides parallel. *Flowers.*—Female flowers only in axils of lower leaves, male flowers together with female flowers in axils of the upper leaves; bracts present; styles *c.* 1·5 mm long, erect, deciduous; stamens with filaments much longer than fruit; pollen grains 18 μ in diameter, exine pattern baculate. *Plant.*—Known specimens evidently aquatic, with upper leaves in rosettes. *Leaves.*—Submerged leaves linear, 1-nerved, sometimes with 2 free veins, upper leaves spathulate, 3- to 5-nerved, 5·5–7 mm long, 2·4–2·9 mm broad.

General Distribution.—Australia—Victoria.

Specimens Seen

AUSTRALIA—VICTORIA: Swan Hill, Murray R., *J. G. Luehmann*, 1890 (MEL); Shire of Lowan, W. Vic., *St. Elvey D'Alton* (MEL); Hawkesdale, *H. B. Williamson*, Dec. 1903 (BRI); Yarra Yarra, Vic., *F. Mueller* (MEL, isotype).

C. cyclocarpa seems most closely related to *C. palustris*. It also has the pits of the reticulations in distinct rows, but not so conspicuously as *C. palustris*. The outline of the fruit whether seen edge on or face on, and the appearance of the wing, however, are quite distinct.

13. C. **palustris** L., Sp. Pl. **2**: 969 (1753).

Figs. 13, 13*A*

C. verna L., Fl. Succ., 2nd Ed., 2 (1755).

Fruit.—Dark brown when ripe, longer than broad (0·75–0·9 mm broad by 0·8–1 mm long), faces flat, pits of reticulations often in distinct rows, thicker through at base than at top, narrowed towards the base, winged, wing colourless and broader at the top and tapering away at the base, commissural groove V-shaped, fairly wide. *Flowers*.—Male and female flowers together in one leaf axil; bracts present, deciduous; styles erect or slightly spreading, 1–2 mm long; stamens up to 5 mm long. *Plants*.—Amphibious, with well-marked rosettes. *Leaves*.—Lower leaves linear, 1-nerved, emarginate, up to 1 mm wide and 2 cm long, rosette leaves orbicular or elliptical, tapering into a broad petiole *c*. 10 mm long by 3–4 mm wide, sometimes 5-nerved.

General Distribution.—North America, Europe, Asia, New Guinea, New Caledonia, Australia.

Specimens Seen

AUSTRALIA—VICTORIA: Springs on the lower Hume's R., *F. Mueller*, Jan. 1874 (MEL); Murray R., Bergeroop, Herb. H. B. Williamson, Dec. 1920 (MEL); Broken R., *V. Say*, 1887 (MEL); Goulburn R., *V. Say* (MEL); Biggara, Upper Murray, *H. B. Williamson*, Nov. 1928 (MEL).

Schotsman (1954) gives reasons for preferring the name "*C. palustris* L." to that of "*C. verna* L." by which it is generally known in Europe. It is fortunate that the name "*C. verna*", erroneously associated with various Australian and New Zealand species, should be dropped.

VI. ACKNOWLEDGMENTS

I wish to thank the Directors of herbaria and museums, and Dr. R. Cooper of the Auckland Museum, who lent specimens and sent information.

In particular I thank Dr. H. Horn af Rantzein of the Naturhistoriska Riksmuseum, Stockholm, for authentic specimens of European species and for copies of the papers by Hegelmaier which were not obtainable in New Zealand.

I also wish to thank Dr. R. Melville of Kew, Mr. W. T. Stern of the British Museum, and Mrs. R. Fenton for information concerning specimens; Miss N. M. Adams of the Botany Division, D. S. I. R., for drawings and assistance with the illustrations; and Mr. N. T. Moar, Botany Division, for the information about pollen.

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Addendum

Since the above was written some further specimens have been collected by R. Mason and N. T. Moar. All are in the Botany Division herbarium, Christchurch.

C. muelleri

NORTH ISLAND: Waikato R., opposite Mare Mare, 6152. SOUTH ISLAND: Kokatahi Valley, 5179; Okarito Lagoon, 5563.

This extends the distribution of the species about 100 miles further down the west coast of the South Island.

C. petriei subsp. *petriei*

NORTH ISLAND: Waikato R. at Mercer, 7009; Waikato R. opposite Mare Mare, 6153; creek from L. Waikare, near Rangiriri station, 6911; Waikato R. at landing between Huntly and Ohinewai, 6802; Waikato R., S. of Huntly, 6330. SOUTH ISLAND: Okarito Lagoon, 5562.

In a month's field work in the Waikato district in November–December 1958 no further specimens of *C. heterophylla* were found.

List of Species

antarctica Engelm. 312
aucklandica sp. nov. 314
brachycarpa Hegelm. 310
capricorni sp. nov. 307
cyclocarpa Hegelm. 324
hamulata Ktzg. 323
heterophylla Pursh emend. Darby var.
  heterophylla 320
muelleri Sond. 304
palustris L. 325
petriei sp. nov. 315
  subsp. *petriei* 316
  subsp. *chathamensis* 317
sonderi Hegelm. 306
stagnalis Scop. 321
umbonata Hegelm. 310

THE AUSTRALIAN SPECIES REFERRED TO *ICHNANTHUS* BEAUV. (GRAMINEAE)

By M. Lazarides*

[*Manuscript received December* 9, 1958]

Summary

The opinion is expressed that the genus *Ichnanthus* Beauv. is represented in Australia by only one species, *I. vicinus* (Bail.) Merr. It is proposed to re-establish in *Panicum* L. three species currently referred to *Ichnanthus* and transfer to it *Ichnanthus muelleri* Hughes. A revised account is given of the species concerned as to taxonomy, distribution, and economics.

I. Introduction

This paper is concerned primarily with defining the Australian species referred to *Ichnanthus* first by Hughes (1923) and generally retained in that genus until recently, when Blake (1958) undertook the study of relationships between genera allied to *Panicum*. Also, an attempt has been made to clarify the status of the group in relation to *Panicum* and to the largely tropical American genus *Ichnanthus*.

The material used in the study comprised that available in the Australian State herbaria, and the collections of the Divisions of Plant Industry, and Land Research and Regional Survey, C.S.I.R.O., Canberra. In the lists of specimens quoted under descriptions these herbaria are referred to under the abbreviations established in the "Index Herbariorum", third edition. Where several specimens from one herbarium are listed the name of the appropriate herbarium is given at the end of a consecutive series. Generally herbarium representation of the species was poor. This is possibly due to their scattered distribution in somewhat remote and underdeveloped areas of the tropics and to their sparse occurrence in a restricted environmental range. Among specimens examined are included collections by the author, who had occasion to observe all species in the field. Also, all specimens cited have been seen.

Ichnanthus vicinus (Bail.) Merr. is here recognized as the only Australian representative of the genus. Of the remaining species involved, *I. majusculus* (F. Muell. ex Benth.) Hughes, *I. pauciflorus* (R. Br.) Hughes, and *I. australiensis* (Domin) Hughes are re-established in, and *I. muelleri* Hughes is transferred to, *Panicum*. The identity of *I. oblongus* Hughes remains obscure and is dealt with separately in this paper.

II. Circumscription of the Genus Ichnanthus Beauv.

The genus *Ichnanthus* Beauv. is based on a specimen collected by Desfontaines in South America. In the original account Beauvois (1812) gives a generic description listing "*Isch. panicoides*", which is figured (Plate xii, Fig. 1). This specimen has not been seen. However, Chase (1911) in a history of the genus remarks that

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* Division of Land Research and Regional Survey, C.S.I.R.O., Canberra.

Beauvois's specimen was not seen by her and writes: "the figure, though slightly inaccurate, is a good illustration of the species, well described and figured by Kunth (Rev. Gram. 2: 245. pl. 34. 1830) under the name *Ichnanthus panicoides*".

Beauvois misinterpreted the structure of the spikelet, describing a "FLOSC. INTERMED. incompletus, abortivus: PALEAE cartilagineae oppositae, aliis flosculis contrariae dispositae". Beauvois's figure well illustrates the paleae of his intermediate floret. Without doubt, these paleae represent the basal appendages to the fertile floret and they are shown as almost half the length of that organ.

The presence of these appendages adnate to the base of a hermaphrodite floret served to discriminate the group from *Panicum*. The circumscription was widened later to include species in which the basal appendages were represented by minute depressions or excavations as well as those possessing distinct membranous appendages. Early authors interpreted the structure of these appendages in various ways and the wide variation occurring in the distinguishing characteristic of the group provided a subject of intense controversy. Consequently, as Chase (1911: 143–4) details, while several authors recognized *Ichnanthus* as a valid and sound genus, almost an equal number upheld its inclusion in *Panicum*, often as a separate section. More recently Hitchcock (1920), though recognizing the genus, observed: "As a genus *Ichnanthus* is less distinct than several groups, such as *Syntherisma*, *Lasiacis*, and *Echinochloa*, that were included by older authors in *Panicum* as sections".

As today accepted, the generic concept of *Ichnanthus* closely follows the description made by Chase (1911: 144) in which the appendages may be either prominent or reduced. As a result a number of the species included deviate from *I. panicoides* Beauv., the nomenclatural type, which has very large appendages. Of the 10 species recorded for North America by Hitchcock (1920), only four possess well-developed appendages, which in each case are less than 1·5 mm long.

Notwithstanding this the group appears to be a natural one. Representatives of the genus are decumbent or prostrate perennials with weak, many-noded culms and broad, flat, sometimes petioled leaf blades, growing in moist or shady situations, often in forest communities. Panicles are almost simple, terminal and axillary, mostly contracted, the few branches only slightly spreading. Spikelets are laterally compressed, shortly and unequally pedicelled, paired, clustered, and more or less appressed to the primary branches, rarely solitary in an open, loose panicle, e.g. *I. ichnodes* (Griseb.) Hitchc. & Chase. The glumes and lower lemma are keeled, shortly aristate, strongly nerved, scabrous or scaberulous on the keel, glabrous, or more often sparsely hispid on the margins and towards the apex.

As so defined, *Ichnanthus* comprises approximately 26 species, all of which with one exception inhabit the tropics of the New World. The majority of these species grow in South America. *I. vicinus*, the only known Old World species, is found in south-east Asia and extends through Malaysia to tropical Australia.

III. The Generic Position of the Australian Species

The examination of a number of specimens belonging to the following: *Ichnanthus vicinus* (Bail.) Merr., *I. panicoides* Beauv., *I. nemorosus* (Swartz) Doell, *I. pallens* (Swartz) Munro, *I. riedelii* (Trin.) Doell, *I. ichnodes* (Griseb.) Hitchc. & Chase, *I. axillaris* (Nees) Hitchc. & Chase, *I. tenuis* (Presl.) Hitchc. & Chase, and the Australian endemic species revealed some distinct discrepancies within the group as a whole, and leads the author to believe that there are two well-marked groups.

The most prominent morphological differences may be found in the structure of the spikelet and panicles. These and related differences are where possible analysed in Table 1 or discussed in the following text.

Table 1

DIFFERENCES BETWEEN ENDEMIC SPECIES AND ICHNANTHUS SENS. STR.

	Australian Endemic Species	*Ichnanthus* sens. str.
Spikelets	Slightly dorsally compressed, long pedicelled	Laterally compressed, shortly pedicelled
Glumes	Semideciduous, rounded on the back, glabrous, smooth, acute or acuminate	Persistent, keeled, usually hispid on the margins or towards the apex, scabrous on the keel and often towards the apex, aristate
Palea (lower)	0·5 mm long or less	Two-thirds the length of its lemma, usually 3–4 mm long
Habit	Annuals or biennials; culms erect, few-noded, wiry; blades linear to linear-lanceolate	Perennials; culms decumbent or prostrate, many-noded, weak; blades lanceolate to lanceolate-ovate, thin, often petioled, sometimes abruptly contracted and almost cordate at the base
Distribution	Dry tropical and warm temperate regions; arid to high rainfall areas; open woodland or sand-hill communities; predominantly sandy soils	Wet tropical regions; very high rainfall areas; moist or shady habitats, usually in forest communities; apparently heavy clayey as well as sandy soils

Furthermore, the Australian endemic species are closely linked by a constant similarity in the structure of the rhachilla and the basal appendages as one analogous unit. The rhachilla is prolonged into a stipe, widening at the apex into an orbicular disk and supporting the two appendages, which are small (consistently about 0·5 mm long), fused to the margins of, but free above, the rhachilla. In *Ichnanthus* sens. str., the appendages may be prominent and wing-like, ranging from 0·5 mm long and membranous in texture as in *I. ichnodes*, to almost 4 mm long and cartilaginous in *I. panicoides*. In these species (as in *I. riedelii*), the appendages are fused to the margins of the rhachilla and free from the fertile floret. In *I. vicinus*, *I. pallens*, *I. tenuis*, *I. axillaris*, and *I. nemorosus*, however, the appendages are minute, hyaline, and adnate to, and sunk into, marginal depressions at the base of the fertile lemma as well as fused to the margins of the rhachilla. In these cases, though the excavations are prominent, the very thin appendages may appear wanting, but in well-matured specimens the contrasting tissues of the lemma and appendages are rather well pronounced.

Species of *Ichnanthus* sens. str. are further characterized by a thickening of the base of the palea which is evident as a distinct protuberance between the depressions or appendages, and is more prominent in those species with excavations than in those with distinct appendages. This feature is not found in the Australian endemic species, in which the base of the fertile floret is wholly enclosed within the concave, orbicular, disk-like apex of the rhachilla.

Also, the panicles of *Ichnanthus* sens. str. usually bear several spikelets which because of their very short pedicles remain appressed to the primary branches. These inflorescences differ from those of the Australian endemic group which possess fewer, more divergent, usually shorter secondary branches with fewer spikelets which are borne on elongated pedicles, and present a more open, looser aspect with the spikelets appearing distant and remote. These characteristics apply to a lesser extent to *Panicum australiense* Domin, in which the reduced inflorescences approach those of *Ichnanthus nemorosus* and small-panicled forms of *I. vicinus*.

IV. Characters of the Australian Group of Species

The characters of *Ichnanthus* sens. str. and the reasons for separating the Australian species from it have been discussed above and are summarized in Table 1. To further clarify the differences between them a summary of the characters shared by the Australian group is given below:

Spikelets lanceolate or elliptic in outline, acute-acuminate; pedicels filiform, the terminals about twice as long as the laterals. *Glumes* glabrous (sometimes the mid nerve pilose towards the apex on the inner surface), nerved, lanceolate or ovate; the lower about half the length of the spikelet or slightly more, separated from the upper one at their points of attachment by a distinct internode 0·5 mm long; the upper as long as the spikelet. *Lower lemma* similar to the upper glume in size, shape, length, and texture, subtending a minute hyaline palea. *Upper lemma* shorter than the spikelet, faintly nerved, acute to subobtuse, ovate to elliptic. *Palea* similar to its lemma in texture, colour, and length, acute to obtuse, ± flat and faintly nerved between the keels. *Appendages* 2, minute, firmly membranous, erect or curved. *Stamens* 3. *Stigmas* plumose, purple. *Caryopsis* elliptic to orbicular in outline, dorsally compressed. Tufted, often short, annual or short-lived perennial grasses with fibrous roots. *Culms* fastigiately branched, glabrous or hairy, usually scaberulous; internodes usually subequal in length; nodes usually bearded. *Leaves* scaberulous, striate, glabrous or hairy with simple or tubercle-based hairs; blades acuminate, flat; ligule a ciliate line; sheaths loosely convolute, usually about half the length of their internodes. *Panicles* loose and open with elongated pedicels or contracted; rhachis, branches, and pedicels slender, glabrous, flattened or angled, scaberulous; pulvini often present.

All four species are distributed throughout tropical regions of Western Australia, the Northern Territory, and Queensland (Fig. 1). *P. australiense* is adaptable to a wider climatic range and extends to the arid interior and to warm temperate areas of these States and South Australia. The remaining species on the other hand are largely confined to a medium to high rainfall belt (25–40 in.) in the northern section of the tropics.

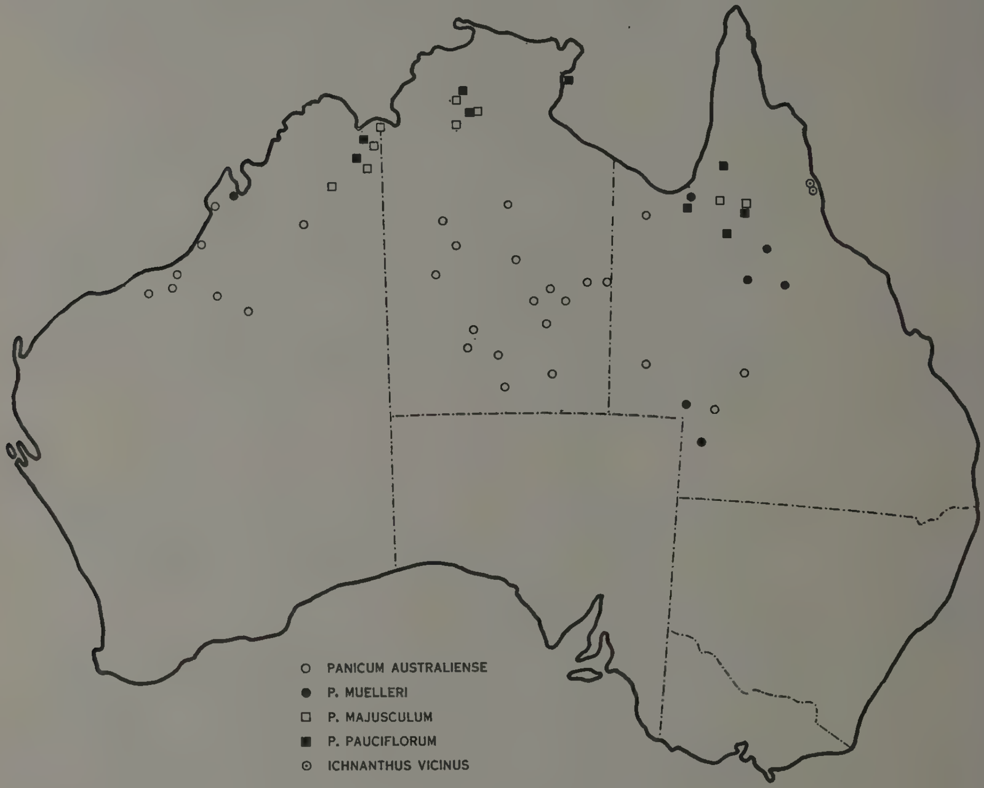

Fig. 1.—Distribution of species.

P. australiense attains some localized prominence in central Australia and adjoining areas of Queensland as a constituent of sandhill floras. Generally, however, the species occur erratically and sparsely, and are rather selective of edaphic conditions, being almost wholly confined to coarse-textured podzolic, red earth, and alluvial soils. *P. pauciflorum* is also known to occur on some gravelly lateritic soils.

P. majusculum and *P. pauciflorum* are known to be grazed. In general, however, the species make little contribution to the value of native pastures.

Malformed spikelets in which the upper lemma and palea are very much elongated and over twice as long as the glumes are a not uncommon feature of most species, particularly *P. pauciflorum.*

KEY TO THE SPECIES

A. Culms 5–25 cm high. Panicles contracted and distinctly overtopped by the subtending leaves, or the upper ones open and shortly exserted.
  B. Culms rarely above 15 cm high, numerous, densely fastigiate. All panicles contracted and distinctly shorter than their subtending leaves. Spikelets 3–4 mm long, less than 1·5 mm wide. Lower glume 3- to 5-nerved. Lateral pedicels to 4 mm long .... 1. *P. australiense*
  BB. Culms 15–23 cm high, sparsely fastigiate. Panicles rarely contracted, shortly exserted or slightly shorter than the subtending leaves. Spikelets 4·5–5·25 mm long, 1·5 mm wide. Lower glume 5- to 7-nerved. Lateral pedicels to 7 mm long .... 2. *P. muelleri*
AA. Culms 20–60 cm high. Panicles loose and open, distinctly exserted. Contracted inflorescences few, becoming loosely expanded.
  C. Spikelets lanceolate-elliptic, acute, 5·5–6·75 mm long and usually 2 mm wide. Upper floret ovate, obtuse, 3 mm long. Lower glume 7- to 9-nerved, acute. Habit stout .... 3. *P. majusculum*
  CC. Spikelets narrowly elliptic, acuminate, 4–5 mm long, 1–1·5 mm wide. Upper floret elliptic, acute, 2·5 mm long. Lower glume usually 5-nerved, acuminate. Habit rather slender .... 4. *P. pauciflorum*

V. DESCRIPTION OF SPECIES

1. **Panicum australiense** Domin, J. Linn. Soc. (Bot.) **41**: 271, Pl. 10, Fig. 7, Pl. 11, Figs. 8–12 (1912); Bibl. Bot. **85**: 309 (1915); *P. pauciflorum* var. *fastigiatum* Benth., Fl. Aust. **7**: 483 (1878); *Ichnanthus australiensis* (Domin) Hughes, Kew Bull. **1923**: 329 (1923); J. M. Black, Fl. S. Aust., Pt. 1, 2nd Ed.: 74 (1948); Gardn., Fl. W. Aust. **1**(1): 261 (1952).

Holotype.—North-west Australia, between Ashburton R. and Yule R., *Dr. E. Clement* (not seen).

Syntypes of Synonym.—In the interior, *McDougall Stuart*; upper Victoria R., *F. Mueller* (MEL); near Alice Springs, *Giles*, May 1875 (MEL). Only the two latter specimens seen.

Low, densely compact annual. *Culms* very numerous, 5–15 cm high (rarely to 25 cm), particularly fastigiate at the upper nodes, mostly geniculate-ascending with oblique laterals, glabrous or hispid with tubercle-based hairs (usually on the upper half of the internodes), smooth or scaberulous, 2- to 4-noded. *Leaves* hispid; *sheaths* hispid with tubercle-based, spreading, whitish hairs; ligule long ciliate; *blades* linear-lanceolate, acuminate, 4–6 cm long and 2–2·5 mm wide, smooth or scaberulous, hispid with scattered, usually tubercle-based hairs especially along the thickened margins, sometimes almost glabrous. *Panicles* numerous, contracted, about 2–3 cm long and up to 1 cm wide, with 2–3 branches and few spikelets, partly enclosed by the subtending sheath and distinctly shorter than their blades; lateral pedicels up to 4 mm long. *Spikelets* elliptic, acute-acuminate, pallid, 3–4 mm long and 1·25 mm wide. *Lower glume* ovate, acute or acuminate, 3- to 5-nerved; *upper glume* and *lower lemma* 5- to 7-nerved, elliptic-ovate, acuminate. Lower palea narrow, acuminate, 0·5 mm long. *Upper floret* 1·5–2 mm long, elliptic, acute to almost obtuse, dark brown at maturity; stipe about 1 mm long; appendages 0·5 mm long, narrow, acute. *Caryopsis* elliptic-orbicular, 1·25 mm long and 1 mm wide, pale brown (Fig. 2).

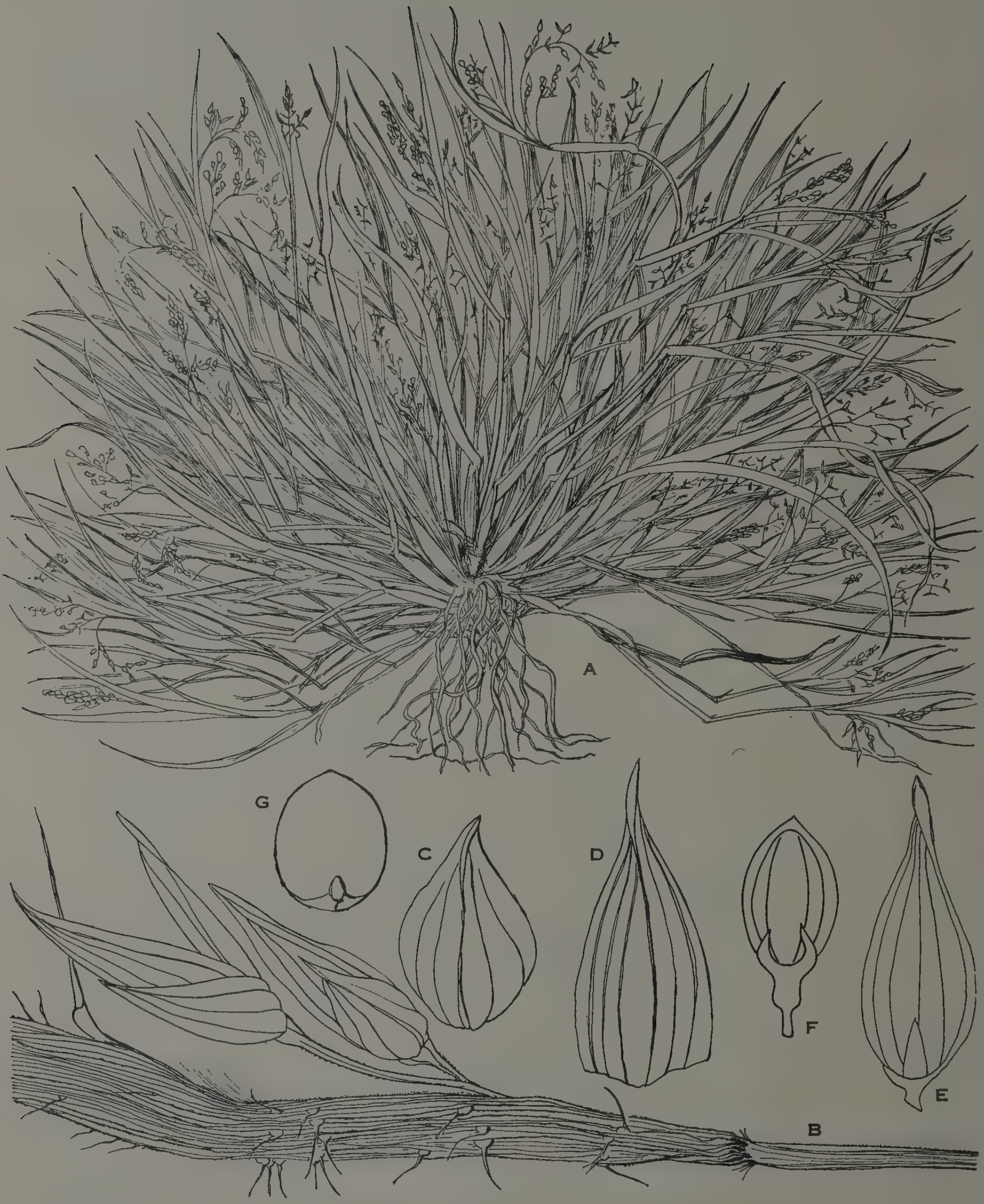

Fig. 2.—*Panicum australiense* Domin from *Lazarides* 5264. *A*, plant. ×½. *B*, portion of panicle showing spikelets, leaf sheath, and blade. ×10. *C*, lower glume. ×12. *D*, upper glume. ×12. *E*, lower lemma from within. ×12. *F*, floret and appendages. ×12. *G*, caryopsis. ×12.

WESTERN AUSTRALIA: Northern Province: Christmas Ck., *A. J. Ewart*, May 1927; Broome, *W. V. Fitzgerald* 134, Apr. 1905; Poondanah siding, E. of Pt. Hedland, *N. T. Burbidge* 651, May 1941; Shaw R., *A. J. Anderson* 317, 24.iv.1937; Warralong siding, Marble Bar railway, *N. T. Burbidge* 858, May 1941; rabbit proof fence, *R. D. Royce* 1620, 14.v.1947; Anna Plains station, *N. T. Burbidge* 1388, 9.vii.1941; between Oakover R. and Canning stock route, *J. N. Casey*, 1954; Jubilee Downs, Fitzroy R., *C. A. Gardner* 10037, 13.iv.1951; Goody Goody, *W. V. Fitzgerald* 278, Apr. 1905 (PERTH); Woodstock, *N. T. Burbidge* 5980, 6.v.1958 (CANB). CENTRAL AUSTRALIA: Between Alice Springs and Charlotte Waters, *Giles*, May 1875 (MEL, PERTH); near Alice Springs, *Giles*, May 1875 (MEL); Narwietooma, *C. A. Gardner* 11592, 10.iii.1953 (PERTH); Simpson Desert Expedition, sand ridge 8 miles NE. of Andado bore, *R. L. Crocker*, 5.vi.1939 (AD); N. of McDonnell Ra.: Plenty R., Marshall R., Milne R., L. Nash, *Lieut. Dittrich*, 1886; near Short's Ra., *M. Stuart* (MEL): 3 miles SW. of McDonnell Downs station, on sandy colluvial slope with *Eucalyptus gamophylla*, *R. A. Perry* 3402, 12.iii.1953; 20 miles E. of Ammaroo homestead, in deep, red sand, *M. Lazarides* 6218, 30.iii.1957; 22 miles WSW. of Argadargada homestead, common on red sandy loam with *Eucalyptus terminalis–Triodia basedowii* open woodland, *M. Lazarides* 5264, 12.v.1955 (CANB); 2 miles E. of No. 2 bore, Hamilton Downs, infrequent in deep red sand, *G. Chippendale* 2002, 12.iv.1956 (BRI). NORTHERN TERRITORY: Upper Victoria R., *F. Mueller* (MEL); 2·3 miles S. of Elliott, *R. A. Perry* 286, 11.vii.1947; 6 miles N. of Hooker's Ck. Mission, on lateritic red, sandy soil, *M. Lazarides* 2921, 24.vi.1952; 30 miles SSW. of Wavehill station, near edge of truncated lateritic desert, *R. A. Perry* 2214, 21.vi.1949; 24 miles S. of Tennant Creek town, *G. Chippendale* 954, 8.iii.1955 (CANB). QUEENSLAND: Burke district: Adel's Grove, Camooweal, widespread on stony ridge and banks of rocky gullies in sandstone country, *A. de Lestang* 234, 18.iii.1946; Mitchell district: S. of Jundah, on low sandhill, *S. T. Blake* 12075, 11.vii.1936; Gregory North district: 30 miles S. of Bedourie, on sandhills, *S. T. Blake* 12285, 21.vii.1936; Gregory South district: 43 miles W. of Windorah, on a sandhill, *S. T. Blake* 12108, 13.vii.1936 (BRI).

The holotype has not been seen but the specimens cited agree with Domin's description and figures; as do also Giles's Alice Springs and Mueller's Victoria River specimens, which are assumed to be syntypes of *Panicum pauciflorum* R.Br. var. *fastigiatum* Bentham.

A characteristic species: the low leafy densely compact habit, the numerous reduced partly enclosed panicles, and the prominently overtopping blades are distinctive features within the group.

Tall forms (24 cm high) in which the panicles are rather elongated and open, and scarcely exceeded by the subtending leaves, e.g. *Fitzgerald* 278, approach *Panicum muelleri*.

2. **Panicum muelleri** (Hughes) Lazar. comb. nov.

Ichnanthus muelleri Hughes, Kew Bull. **1923**: 329 (1923); Gardn., Fl. W. Aust. **1**(1): 261 (1952).

Holotype.—Western Australia, near King Sound, *Mueller* (K ? not seen).

Loosely tufted annual or short-lived perennial. *Culms* 15–23 cm high, geniculately ascending or erect, rather slender, glabrous, 3- to 5-noded; uppermost internode somewhat elongated. *Leaves* hispid, particularly on the under surface, sometimes only pubescent on the upper surface; *sheaths* generally much shorter than their internodes, hispid with tubercle-based, spreading or reflexed hairs; ligule long-ciliate; *blades* linear-lanceolate, acuminate, flat (sometimes partly involute), up to 8 cm long and 2–4 mm wide, hispid with simple or tubercle-based, spreading hairs. *Panicles* loose, ovate in outline, up to 8 cm long, 4–5 cm wide, slightly shorter than or shortly exserted above the subtending leaves, often with contracted, non-exserted, axillary panicles; lateral pedicels usually 3–5 mm long. *Spikelets* elliptic, acuminate, 4·5–5·25 mm long, 1·5 mm wide. *Lower glume* acuminate, ovate, 7-nerved (the laterals sometimes indistinct); *upper glume* lanceolate-elliptic, acuminate, 7- (rarely 9-) nerved; *lower lemma* 7-nerved; *lower palea* distinctly bifid, 0·5 mm long. *Upper floret* elliptic, almost obtuse, 2–2·5 mm long, golden in colour, turning dark brown with maturity; stipe 1 mm long; appendages narrow, acute, 0·5 mm long or less. *Caryopsis* ovate-elliptic to suborbicular in outline, 2 mm long, 1·25 mm wide, pale brown (Fig. 3).

WESTERN AUSTRALIA: Northern Province: King Sound, *W. W. Froggatt*, 1888 (NSW). QUEENSLAND: Without locality, *T. L. Bancroft?*, Qld. Herbarium No. 006925 (BRI); Burke district: near head of Poison Ck., 90 miles N. of Hughenden, on compact sand in *Eucalyptus* forest, *S. T. Blake* 8569, 11.iv.1935 (BRI, NSW); Normanton, on sand in shallow channels and depressions on low barren ridge slopes, *Blake* 9034, 20.v.1935 (BRI); 19 miles E. of Richmond township, rare on deep yellow coarse gravelly podzolic soils with *Eucalyptus terminalis* and *Aristida* spp., *M. Lazarides* 4472, 21.vi.1954 (CANB); Mitchell district: Eurunga, *J. R. Chisholm*, Feb. 1916 (BRI); Gregory North district: Mt. Howitt station, 80 miles W. of Eromanga, on drift sand with *Eragrostis eriopoda*, *S. T. Blake* 11937, 4.vii.1936 (BRI); Currawilla, about 100 miles W. of Windorah, in loose red brown sand on crest of sandhill with *Triodia*, *Eriachne*, and *Plagiosetum*, *S. L. Everist* 3950, 10.vi.49 (BRI, CANB).

The circumscription followed here is based on Hughes' description, as no specimen of Mueller's King Sound collection has been seen.

Its closest affinities are with *P. australiense*, from which it differs in its larger spikelets, looser usually taller habit, 5- to 7-nerved (not 3- to 5-nerved) lower glume, and opened slightly exserted panicles (not prominently exceeded by the uppermost sheaths). Those forms with numerous branching culms and in which axillary panicles are predominant (e.g. *Blake* 11937 and *Lazarides* 4472) bear a very close superficial resemblance to that species. The shape, size, and nervature of its spikelets, however, are closer to those of *P. pauciflorum*.

3. **Panicum majusculum** F. Muell. ex Benth., Fl. Aust. **7**: 482 (1878); Domin, Bibl. Bot., Stuttgart **85**: 310 (1915); Ewart and Davies, Fl. North. Territ., 36 (1917); *Ichnanthus majusculus* (F. Muell. ex Benth.) Hughes, Kew Bull. **1923**: 329 (1923); Gardn., Fl. W. Aust. **1**(1): 262 (1952).

Holotype.—Northern Territory, Victoria R., *Elsey* (K?) (isotype in MEL). Only the latter specimen seen.

Loosely tufted annual or short-lived perennial. *Culms* several, 25–60 cm high, rather stout, erect or geniculately ascending, branched with up to 4 culms from each node, glabrous or hirsute or hispid with tubercle-based, sometimes simple, slender, spreading hairs; 4- to 6-noded; uppermost internode very much elongated; nodes sometimes glabrous. *Leaves* glabrous or hairy; *sheaths* usually less than half the length of their internodes, densely hispid or hirsute with tubercle-based hairs, rarely glabrous and then often with scattered tubercles or hairs on the margins; *blades* linear-lanceolate, long acuminate, 8–12 (rarely 15) cm long and 2–4 (rarely 5) mm wide, densely hirsute or hispid with slender, tubercle-based (sometimes simple) hairs, rarely glabrous. *Panicles* loose and open, distinctly exserted, ovate in outline, 8–10 cm long and 4–6 cm wide, axillary panicles if present smaller but

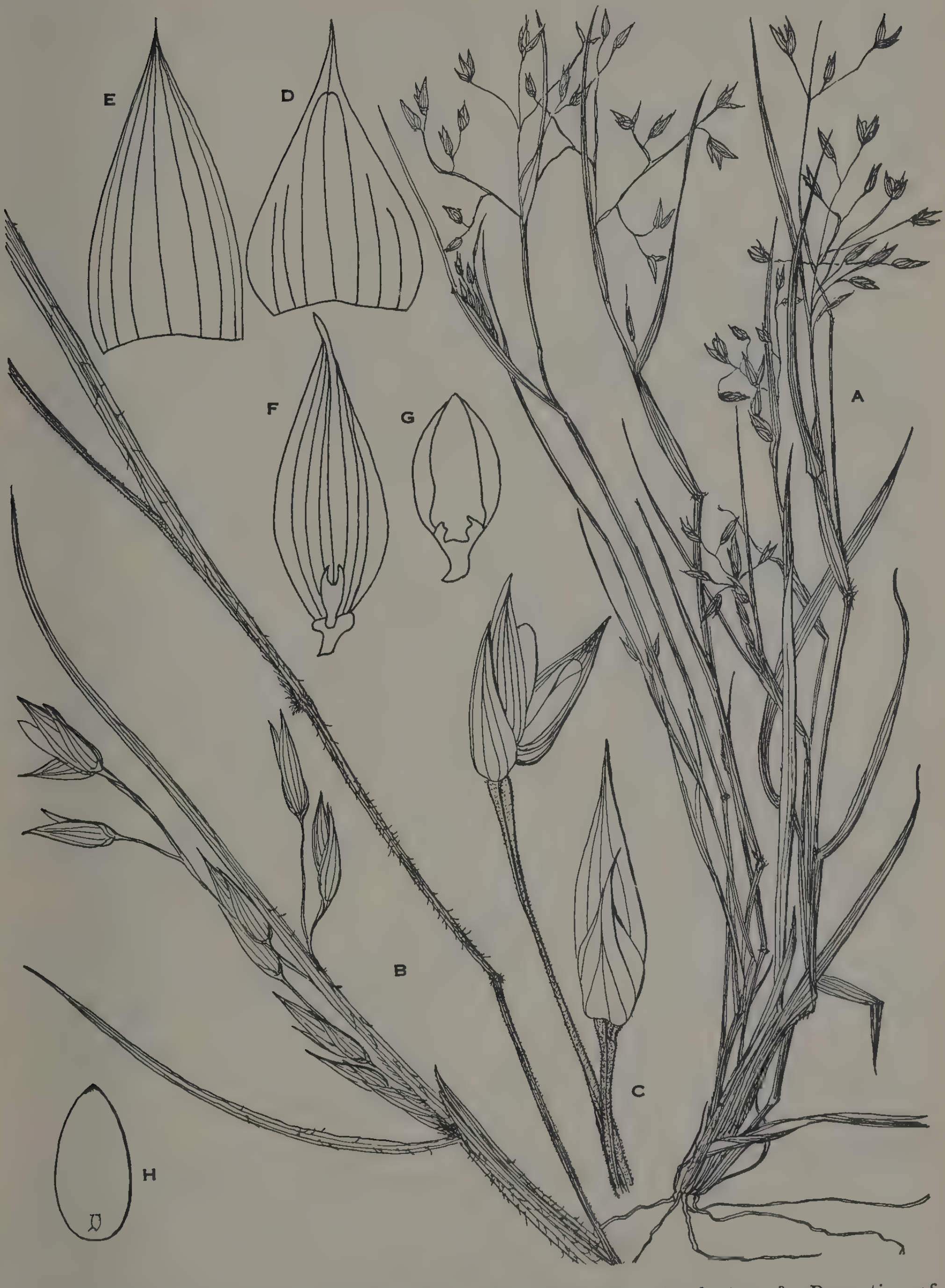

Fig. 3.—*Panicum muelleri* (Hughes) Lazar. from *Blake* 8569. *A*, plant. ×⅜. *B*, portion of panicle, showing culm, leaf sheath, and blade. ×4. *C*, spikelets. ×10. *D*, lower glume. ×10. *E*, upper glume. ×10. *F*, lower lemma from within. ×10. *G*, floret with appendages. ×10. *H*, caryopsis. ×12.

loose; lateral pedicels 4–10 mm long. *Spikelets* lanceolate to lanceolate-elliptic, 5·5–6·75 mm long and usually 2 mm (1·75–2·75) wide, acute, purplish when young becoming pale yellow at maturity. *Lower glume* broadly ovate, acute, 7- to 9-nerved (the laterals sometimes indistinct); *upper glume* and *lower lemma* lanceolate, acuminate, 7- to 9-nerved; *lower palea* 0·5 mm long, acute or emarginate. *Upper floret* broadly ovate to ovate-elliptic, almost obtuse, 2·75–3 mm long, faintly 5-nerved, dark brown or yellow at maturity; stipe stout, 0·5 mm long; appendages narrow, acute, 0·5 mm long. *Caryopsis* broadly ovate to orbicular in outline, 1·5–2·5 mm long, obtuse, pale brown (Fig. 4).

WESTERN AUSTRALIA: Northern Province: Spring Ck., near Button's Gap, between Wyndham and the Kimberley Research Station, *N. T. Burbidge* 5679, 10.iv.1958; E. Kimberley, on coarse sandy soil, *E. C. B. Langfield* 367, 27.ii.1955; 15 miles E. of Carlton station, with *Eucalyptus tectifica–E. grandifolia* open forest on sandy soil on limestone, *R. A. Perry* 2659, 29.vii.1949; 13·5 miles NW. of Elgie Cliffs homestead, occasional on sandy soil, *M. Lazarides* 5105, 17.iv.1955; 10 miles SW. of Denham River homestead, occasional on yellow, gravelly sand with *Eucalyptus grandifolia* and *Aristida hygrometrica*, *M. Lazarides* 5051, 15.iv.1955 (CANB). NORTHERN TERRITORY: Victoria R., *Elsey* (isotype in MEL); Northern Territory, *Gilruth and Spencer*, Jul.–Aug. 1911 (AD); Katherine R., *H. J. Maynard*, Mar. 1953 (PERTH); Katherine, *H. J. Tyack Bake* No. 15, 15.iii.1943, and May 1943 (BRI); 10 miles NNE. of Katherine township, in cultivation on sandy levee soil, *M. Lazarides* 2758, 11.v.1952; Experimental Station, Katherine, sandy soils on river bank, *W. Hartley* 093, 22.iii.1946; "Manbuloo", Katherine, river bank, *F. W. Hely* H 289, Jan. 1943 (CANB). QUEENSLAND: Cook district: Gilbert R., *C. T. White* 1458, Feb. 1922, and *N. A. R. Pollock* (BRI); Burke district: 10 miles NW. of Croydon township, occasional on deep, sandy, yellow podzolic soil with *Eucalyptus polycarpa* and *Aristida hygrometrica, M. Lazarides* 4760, 21.vii.1954 (CANB).

A variable species where the pubescence of the foliage is concerned. The leaves and sheaths of the isotype, though tubercled, are almost glabrous. However, hispid or hirsute forms are equally as common. Where apparently glabrous forms do occur, the careful examination of well-matured blades and sheaths often reveals scattered tubercles and tubercle-based hairs. Both glabrous and hairy conditions may be found on the same plant. Under these circumstances, *Panicum majusculum* var. *pilosum* Domin (1915: 310, Fig. 68), if correctly placed in this species (the type has not been seen), does not seem to deserve varietal rank.

Lazarides 4760 is a semi-prostrate, perennial, profusely branching form with numerous, fastigiate culms at each node. Field observations suggest the possibility that the atypical condition was stimulated by abnormal rainfall following severe grazing.

Panicum majusculum is rather distinctive owing to the shape and size of its spikelets, which are the largest in the group.

4. **Panicum pauciflorum** R. Br., Prod., 191 (1810); Ewart and Davies, Fl. North. Territ., 38 (1917). *Ichnanthus pauciflorus* (R. Br.) Hughes, Kew Bull. **1923**: 330 (1923).

Holotype.—Northern Territory, Gulf of Carpentaria, *R. Brown* (BM) (isotype in MEL). Only the latter specimen seen.

Loosely tufted, rather slender annual or short-lived perennial. *Culms* 20–45 cm high, sometimes somewhat geniculate, often only sparsely branched, 3- to 4-noded, often thin and weak, hirsute with long, tubercle-based, slender hairs, more

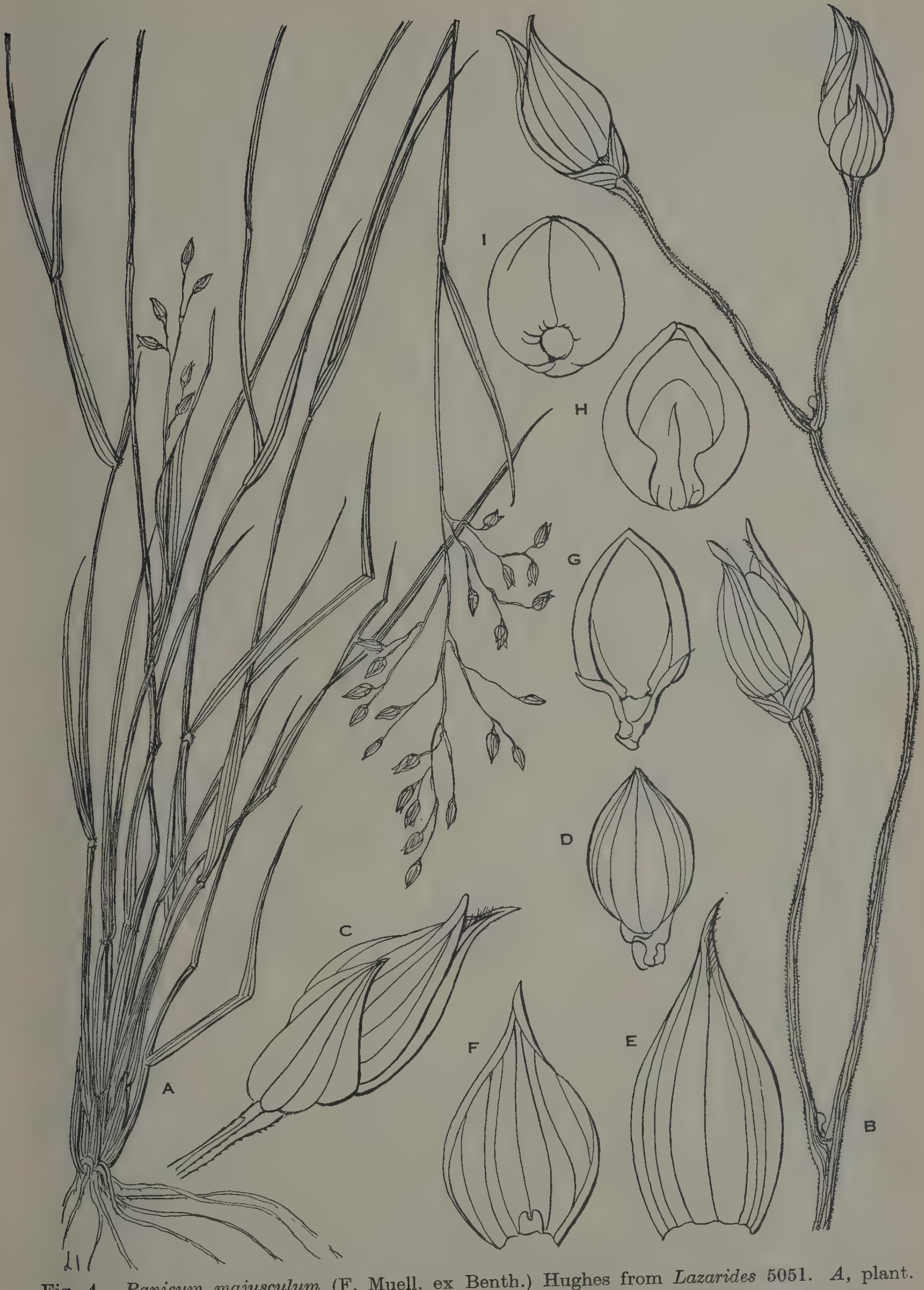

Fig. 4.—*Panicum majusculum* (F. Muell. ex Benth.) Hughes from *Lazarides* 5051. *A*, plant. ×½. *B*, portion of panicle. ×4. *C*, spikelet. ×6. *D*, lower glume. ×6. *E*, upper glume from within. ×6. *F*, lower lemma from within. ×6. *G*, floret with appendages. ×6. *H*, palea from within. ×8. *I*, caryopsis. ×8.

often glabrous; uppermost internode elongated; nodes almost glabrous. *Leaves* hairy; *sheaths* hirsute or hispid with tubercle-based, spreading hairs, mostly less than half the length of their internodes, sometimes closely convolute; *blades* linear-lanceolate, acuminate, 5–10 cm long and 1·5–3 mm wide, hirsute with simple or tubercle-based hairs, often only the upper surface with scattered long, very slender, simple hairs. *Panicles* exserted, ovate in outline, 6–8 cm long and 2–4 cm wide (rarely larger), loose and open, usually with few, shortly exserted, axillary inflorescences; divisions of the panicle very slender; lateral pedicels 3–7 mm long. *Spikelets* narrowly elliptic, acuminate, 4–5 mm long and 1–1·5 mm wide. *Lower glume* ovate, acute to acuminate, 5- or ±7-nerved; *upper glume* and *lower lemma* lanceolate-elliptic, acuminate, 7- (rarely 9-) nerved; *lower palea* less than 0·5 mm long, narrow, acuminate or minutely emarginate at the apex. *Upper floret* elliptic, acute, faintly 5- to 7-nerved, 2·5–2·75 mm long; stipe rather slender, 0·5–0·75 mm long. *Caryopsis* elliptic-orbicular in outline, obtuse, 1·5 mm long and 1 mm wide (Figs. 5, 6).

WESTERN AUSTRALIA: Northern Province: Spring Ck., near Button's Gap, between Wyndham and the Kimberley Research Station, *N. T. Burbidge* 5681, 10.iv.1958; 6 miles SW. of Denham River homestead, occasional in creek lines, *M. Lazarides* 5047, 5047A, and 5047B, 15.iv.1955 (CANB). NORTHERN TERRITORY: North coast, *R. Brown*, 1802–5 (MEL); 20 miles from Katherine on Alice Springs road, on disturbed, sandy ironstone soil, *W. Hartley* 0222, 23.iii.1946; 10 miles NNE. of Katherine township, in sandy soil on river levee, *M. Lazarides* 2759, 11.v.1952 (CANB). QUEENSLAND: Cook district: Gilbert R., *L. Brass* 1717, Feb. 1927; Forest Home station, on sand ridges, *L. Brass* 1808, 15.ii.1931; 15 miles S. of Dunbar, *F. W. Whitehouse* (BRI); Burke district: 2 miles S. of Normanton township, occasional on gravelly lateritic soil, *M. Lazarides* 4264, 6.iii.1954; 12 miles N. of Esmeralda homestead, common in sandy soil in seepage area with *Pandanus* spp., *M. Lazarides* 4738, 18.vii.1954 (CANB).

The circumscription followed here is based on R. Brown's specimen in the National Herbarium of Victoria, Melbourne, which is presumed to be an isotype. Brown's type material was, according to his manuscript notes at the British Museum (Natural History), collected on Morgan's Island on the north coast of Arnhem Land (Burbidge 1955, 1956). This is presumably the specimen listed by Bentham (1878: 483) as "Islands of the Gulf of Carpentaria". Since the distribution of Brown's collections was not completed until after Bennett's death in 1876 (Burbidge 1956), it is almost certain that Brown's specimen at Melbourne was not only seen by Bentham but is a portion of the original collection.

Bentham's description of *Panicum pauciflorum* applies more nearly to his variety *fastigiatum* = *P. australiense* Domin than it does to *Panicum pauciflorum* R. Br.

R. Brown's specimen at Melbourne differs from the remaining collections cited in being smaller (22 cm high) and more hirsute on the internodes, and in its prominently 7-nerved lower glume and 9-nerved upper glume and lower lemma.

Annual and perennial forms vary considerably in habit and bear little superficial resemblance to each other. Annual plants are normally sparsely branched with few panicles. Perennial specimens (e.g. *Lazarides* 4738) on the other hand branch freely at the nodes, which results in numerous fastigiate culms and a corresponding increase in inflorescences.

Lazarides 5047B is a very short form, closely resembling *P. muelleri* in form and spikelet structure but differing in its prominently exserted panicles.

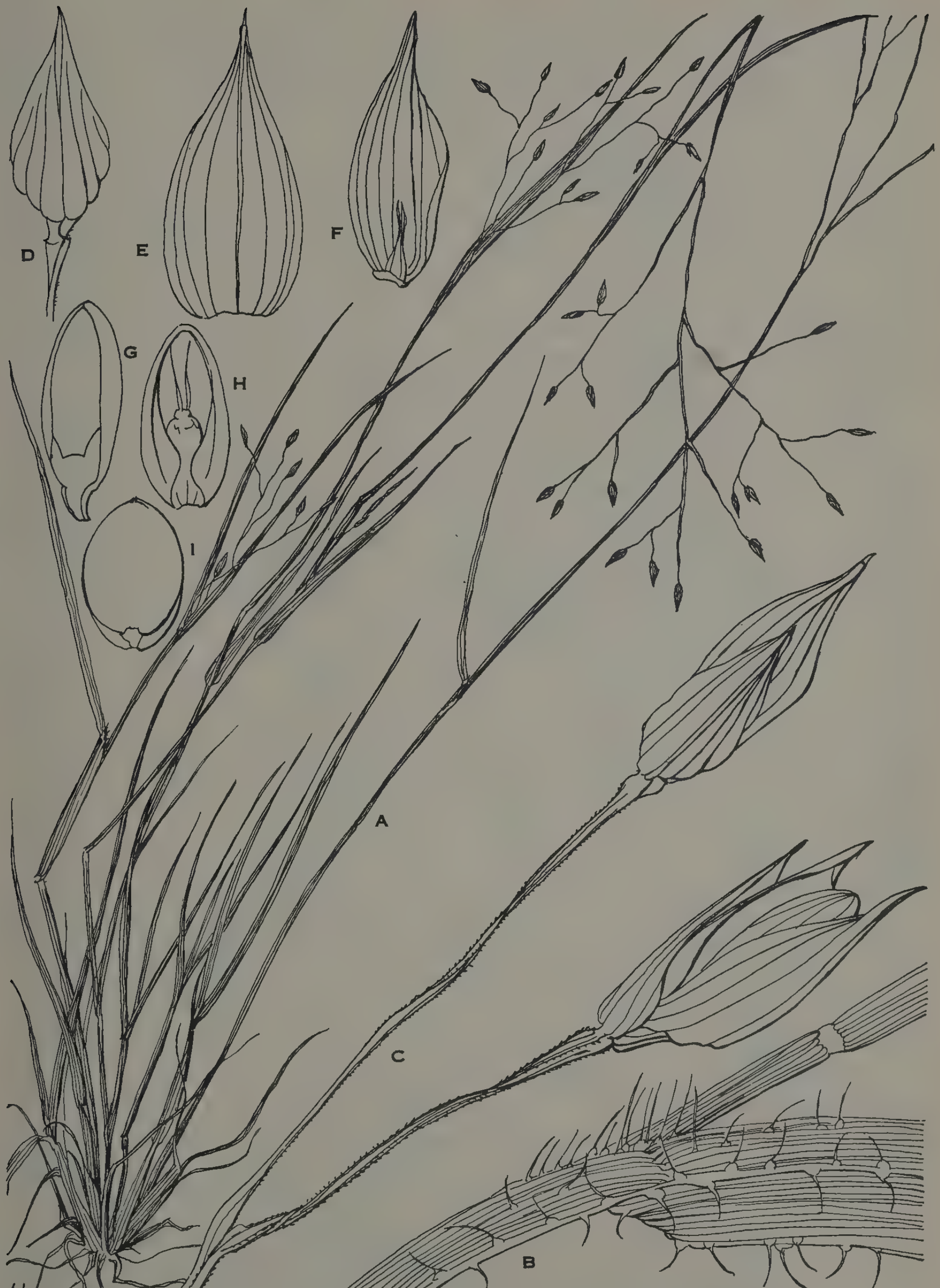

Fig. 5.—*Panicum pauciflorum* R. Br. (annual form) from *Lazarides* 4264. *A*, plant. ×½. *B*, portion of culm with leaf sheath and blade. ×10. *C*, spikelets. ×10. *D*, lower glume. ×10. *E*, upper glume. ×10. *F*, lower lemma from within. ×10. *G*, floret with appendages. ×10. *H*, palea from within. ×10. *I*, caryopsis. ×10.

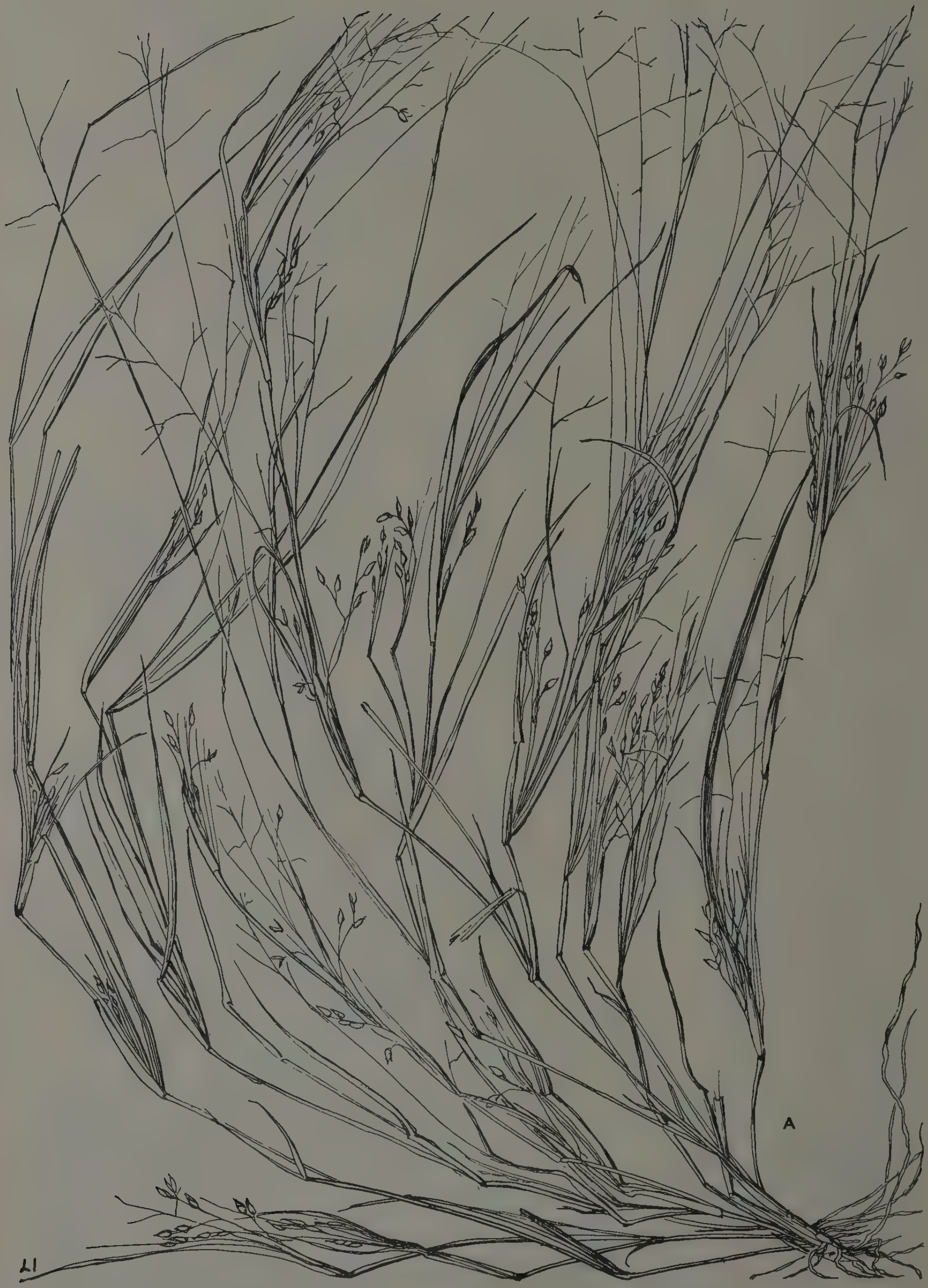

Fig. 6.—*Panicum pauciflorum* R. Br. (perennial form) from *Lazarides* 4738. *A*, plant: ×½.

P. pauciflorum is allied to *P. majusculum*, but differs in its smaller, narrower, elliptic, acuminate (not lanceolate, acute) spikelets and fewer-nerved lower glume. Annual forms are rather easily distinguished by their fewer, slightly branched culms and by their usually slender habit.

VI. ICHNANTHUS VICINUS (Bail.) Merr.

In order to facilitate the comparative study of representatives of both *Panicum* and *Ichnanthus* groups, the inclusion in this paper of a description of *I. vicinus* seems advisable.

Ichnanthus vicinus (Bail.) Merr., Philipp. J. Sci. **4**: xx, 367 (1922); *Panicum vicinum* Bail., Syn. Queensl. Fl., Suppl. **3**: 82 (1890).

Holotype.—Queensland, Harvey Ck. (headwaters of Russell R.) in or near water, *F. M. Bailey* No. 22 (holotype in BRI, isotype in MEL).

Decumbent perennial. *Culms* trailing for several feet, the erect flowering culms 15–45 cm high, pubescent with long, very slender, spreading, simple or tubercle-based hairs, the tubercles usually in longitudinal series between the striations; internodes subequal; nodes pubescent. *Leaves* glabrous or hairy; *sheaths* usually loose, about half the length of their internodes, glabrous or pubescent like the culms, hyaline on one margin, villous with tubercle-based hairs on the other; ligule membranous ciliate; *blades* 3–8 cm long and 1–2 cm wide, acuminate, puberulous to shortly hispid with usually tubercle-based hairs, usually scaberulous on the nerves and thickened margins. *Panicles* contracted and rather dense, narrowly elliptic in outline, up to 15 cm long and about 2 cm wide; rhachis, branches, and pedicels slender, scabrous or scaberulous, compressed, pubescent like the culms, the branches about 3 cm long (the lower sometimes longer), the pedicels up to 3 mm long. *Spikelets* narrowly elliptic, 4·5–6 mm long and 1–1·5 mm wide, gaping at maturity. *Glumes* and *lower lemma* firmly membranous, with scarious margins; *lower glume* about two-thirds the length of the spikelet, ovate-elliptic, 3- to 5-nerved (the laterals sometimes indistinct), smooth (sometimes scaberulous towards the tip or scabrous on the nerves), glabrous or pilose with tubercle-based hairs, the awn stout, scabrous, about 1·5 mm long; *upper glume* as long as the spikelet, lanceolate-elliptic, acuminate or shortly aristate, prominently 5-nerved, with scattered, tubercle-based hairs especially near the scarious margins. *Lower lemma* slightly shorter than the spikelet, lanceolate-elliptic, acute to acuminate, 5-nerved, glabrous, smooth or scaberulous on the keel towards the tip; *lower palea* about 3·5 mm long, hyaline, acute, 2-keeled. *Upper floret* narrowly elliptic, 2–2·5 mm long, obtuse; stipe slender, 0·5 mm long; appendages 2, thinly membranous or hyaline, adnate to and depressed into the base of the upper lemma near the margins (Fig. 7).

QUEENSLAND: Cook district: Harvey Ck. (headwaters of Russell R.), in or near water, *F. M. Bailey* 22 (holotype in BRI, isotype in MEL); Mt. Bartle Frere, in rain-forest, 200–500 ft, *S. T. Blake* 9811, 4.x.1933 (BRI, NSW), and *W. Flecker*, 2.vi.1935 (BRI). TERR. OF NEW GUINEA: Western Highlands district: near Mount Hagen Station, 5600 ft, *R. D. Hoogland* and *R. Pullen* 5975, 21.viii.1956 (CANB). TERR. OF PAPUA: Central district: about 20 miles N. of Port Moresby, alt. *c*. 1500 ft, *L. S. Smith* N.G. 21, 1944 (BRI). Northern district: near L. Ridubidubina, *R. D. Hoogland* 4490, 10.viii.1954 (CANB). BRITISH NORTH BORNEO: Mt. Kinabalu, Dahobang R., in spray of falls, *J. and M. S. Clemens*, Jan. 1933 (BRI).

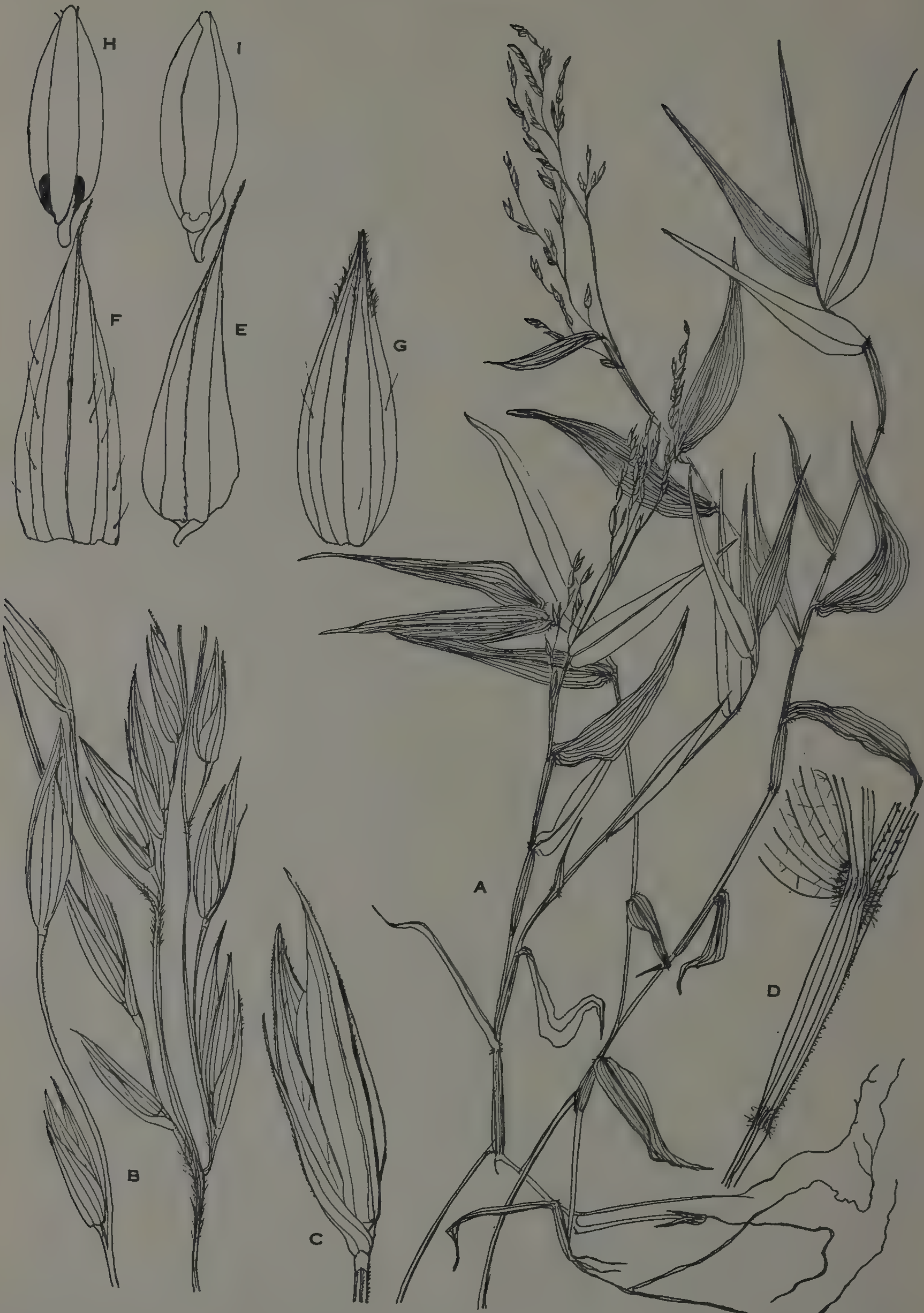

Fig. 7.—*Ichnanthus vicinus* (Bail.) Merr. from *Blake* 9811. *A*, plant. ×½. *B*, portion of panicle. ×5. *C*, spikelet. ×10. *D*, portion of culm, leaf sheath, and blade. ×10. *E*, lower glume. ×10. *F*, upper glume. ×10. *G*, lower lemma. ×10. *H*, floret with appendages. ×10. *I*, palea from within. ×10.

This species was originally described by F. M. Bailey as *Panicum vicinum*. Some botanists, including Bailey (1902) and Domin (1915), treated it as conspecific with *Ichnanthus pallens* (Swartz) Munro ex Benth. from tropical America, from which it differs in its larger spikelets and sparser panicles with fewer, shorter primary branches.

Particularly robust forms are not uncommon in equatorial areas. *Hoogland and Pullen* 5975 is distinctive by virtue of its large blades (10 cm long and about 3 cm wide) and stout, wiry flowering culms 135 cm high with elongated internodes.

I. vicinus is widely distributed throughout the eastern hemisphere, growing in moist situations. In Australia, it is confined to rain-forest communities in very high rainfall areas of north-eastern Queensland.

VII. Ichnanthus oblongus Hughes

Hughes (1923: 328) described this species from a single specimen from Percy Island collected by Cunningham. Apparently the type is rather poor, for Hughes gives only a scanty description and does not figure the species. This specimen, which is located at either the Kew Herbarium or the herbarium of the British Museum (Natural History), has not been seen.

Cunningham's specimen is cited by Bentham (1878: 490) under *Panicum trachyrachis* Benth. var. *tenuior* Benth. along with three other collections. Of these, Peak Downs, *F. Mueller*, and Springsure, *Wuth*, were described by Domin (1911) as *Panicum benthamii* (*P. benthami*) (syntypes in MEL) which was regarded by Hughes (1923: 324) as synonymous with *P. queenslandicum* Domin. Cunningham's specimen or the remaining collection, Brisbane River, *Bailey*, cannot be located in Australian herbaria.

In the original description, Hughes described the structure of the spikelet as: "Glumae inaequales; inferior 2 mm longa; superior 2·5 mm longa. Anthoecium inferum ad valvam spiculam aequantem reductum. Anthoecium superum 3 mm longum appendices 0·3 mm longo incluso". This comment is also added: "With some hesitation, this species is included in *Ichnanthus*. The basal appendage is not very obvious and may be only analogous to the slightly elongated internode found in *Panicum capillipes* Benth. and also in *P. stipitatum* Nash, from North America". The comparative sizes of glumes and both lemmas, as described by Hughes, are certainly unique within her group of *Ichnanthus* species, and rather distinctive among Australian *Panica*, and would suggest an affinity to *Panicum seminudum* Domin or *P. simile* Domin.

In May 1956, the author visited Middle Percy Island (largest of the group) with a view to collecting further material of the species. Unfortunately, no specimens were seen which agreed with Hughes's description. As far as is known, the species has not been collected since the type collection was made. Until the type can be examined, the correct application of the name *I. oblongus* Hughes must remain uncertain.

VIII. Acknowledgments

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INDEX

PAGE

- Baker, G.—
  - Contrast in the Opal Phytolith Assemblages of Two Victorian Soils 88
  - Opal Phytoliths in some Victorian Soils and "Red Rain" Residues 64
- Barlow, B. A.—
  - Chromosome Numbers in the Casuarinaceae 230
  - Polyploidy and Apomixis in the *Casuarina distyla* Species Group 238
- Bieleski, R. L.—
  - Factors Affecting Growth and Distribution of Kauri (*Agathis australis* Salisb.). I. Effect of Light on the Establishment of Kauri and of *Phyllocladus trichomanoides* D. Don 252
  - II. Effect of Light Intensity on Seedling Growth 268
  - III. Effect of Temperature and Soil Conditions 279
- Bogong High Plains, Ecology. I, II 12, 34

- *Callitriche* in Australia and New Zealand 295
- Carr, D. J., and Carr, Stella G. M.—
  - Developmental Morphology of the Floral Organs of *Eucalyptus*. I. The Inflorescence 109
- Carr, Stella G. M., and Turner, J. S.—
  - Ecology of the Bogong High Plains. I. The Environmental Factors and the Grassland Communities 12
  - II. Fencing Experiments in Grassland C 34
- Carr, Stella G. M.—
  - *See also* Carr, D. J. 109

PAGE

- *Casuarina distyla* Species Group, Polyploidy and Apomixis in .. 238
- Casuarinaceae, Chromosome Numbers in 230
- *Chara gymnopitys*, Sporeling of, Development and Morphology 1

- *Eucalyptus*, Morphology of Floral Organs. I 109

- *Gastrodia sesamoides* and its Endophyte 225
- Germination of *Chara gymnopitys*. I 1
- Groenvlei, a South African Coastal Fen, Stratigraphy and History 142
- Growth and Distribution of Kauri, I–III 252, 268, 279

- *Ichnanthus* Beauv., Australian Species Referred to 328
- Inflorescence, of *Eucalyptus*, Development and Morphology 109

- Johnston, R. D.—
  - Control of Water Movement by Stem Chilling 97

- Kauri, Growth and Distribution of. I–III .. 252, 268, 279

- Lazarides, M.—
  - Australian Species Referred to *Ichnanthus* Beauv. (Gramineae) 328

- McLennan, Ethel I.—
  - *Gastrodia sesamoides* R.Br. and its Endophyte 225
- Martin, A. R. H.—
  - Stratigraphy and History of Groenvlei, a South African Coastal Fen 142

PAGE

Mason, R.—
Callitriche in Australia and New Zealand 295
Morphology of Floral Organs of Eucalyptus. I 109
Opal Phytoliths, Assemblages of Two Victorian Soils 88
Opal Phytoliths, in Victorian Soils and "Red Rain" Residues 64
Polyploidy and Apomixis in the *Casuarina distyla* Species Group 238

Ross, Mary M.—
Morphology and Physiology of Germination of *Chara gymnopitys* A. Braun. I. Development and Morphology of the Sporeling 1

PAGE

Sarcomenia Group of the Rhodophyta, Studies 168

Shepley, E. Ann—
See Womersley, H. B. S. . . 168

Stem Chilling, in Control of Water Movement (in plants) . . 97

Turner, J. S.—
See Carr, Stella G. M. 12, 34

Water Movement (in plants), Control by Stem Chilling . . 97

Womersley, H. B. S., and Shepley, E. Ann—
Studies on the *Sarcomenia* Group of the Rhodophyta . . 168